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THE GENETIC RELATIONS OF PLANT COLORS IN MAIZE

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Under the designation "plant colors" are included the colors other than those related to chlorophyll, commonly seen in, but not limited to, such external plant parts of maize as the culm, the staminate inflorescence, the husks, the leaf sheaths, and to some extent the leaf blades. In contrast to this group are colors and color patterns related to chlorophyll or associated with the pericarp and the cob, the silks, the endosperm, the aleurone. The colors included in the group considered here are due to water-soluble pigments, but the same is true of some of the other color groups named above. Moreover, colors of the chlorophyll group (Lindstrom, 1918) are found in the same plant parts as are the "plant" colors considered in this account. The plant colors as a whole are closely interrelated, but they are closely related also to aleurone colors and to certain of the silk and pericarp colors. It is obvious, therefore, that, while this classification is a more or less natural one, it is based primarily on convenience.

The term "genetic relations" in the title to this memoir is to include not merely an account of the genetic analysis of the material at hand by means of hybridization experiments — tho that constitutes the greater part of the paper — but also some consideration of the variations of the several color types induced by or associated with environmental diversities. Some little attention to matters of this kind was made necessary by the fact that presumably homozygous material exhibited marked variations in extent and intensity of pigmentation when grown under diverse conditions. Since, as will be apparent later, the principal differences between certain of the color types under investigation are apparently quantitative ones, and since the materials at best exhibit no little complexity with respect to factorial interrelations of a genetic nature, little progress could have been made without some notion of the response of particular color types to certain factors of the environment. But this study has

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been wholly subsidiary to the main purpose, namely, a genotypic analysis of the color types under observation. The writer's realization of the superficial nature of the environmental studies reported in this account in no way weakens his belief in the importance of acquiring an accurate knowledge of the chemistry of the pigments concerned and of instituting fundamental investigations into the physiology of their development — problems that must await the interest and effort of other workers.

The studies reported here were begun in a small way in 1909 and have been continued, along with other problems in the genetics of maize, to the present time. The work was conducted at the University of Nebraska and supported by funds of that institution from 1909 to 1914. During 1911 facilities for growing and studying a considerable part of the cultures then in hand were generously afforded the writer by the Bussey Institution at Harvard University. Since 1914 the work has been conducted at Cornell University.

During these years, the writer has been assisted by a number of persons, among whom he desires to mention particularly Dr. E. W. Lindstrom and Dr. E. G. Anderson. Some data from the records of students associated with the writer are included in this account. The cultures giving these borrowed data are indicated in the tables by initial letters preceding the pedigree numbers, as follows: A = E. G. Anderson, L = E. W. Lindstrom, and S = Sterling H. Emerson.

The illustrations are from water-color drawings by C. W. Redwood, Miss Carrie M. Preston, and Miss Bernice M. Branson.

PREVIOUS INVESTIGATIONS

So far as the writer is aware, little work with the plant colors of maize has been reported previous to this time. Webber (1906) reported the results of studies of the interrelations of aleurone, silk, anther, and glume colors, with the conclusion that color in all these parts is closely correlated but that there are definite breaks in the correlation. This conclusion, in terms of present-day usage, is apparently equivalent to the idea of close linkage with some crossing-over. East and Hayes (1911) identified certain aleurone-color genes, which are shown in the present account to be related to plant colors as well as to aleurone colors, and reported data concerning the inheritance of silk and anther colors. The writer (Emerson, 1918) added another aleurone-color pair also known to

be concerned in plant-color development. He had earlier (1911) announced some of the plant colors discussed in the present paper and placed on record some evidence as to their genetic behavior. Gernert (1912) described types of maize that differ widely in color of anthers, glumes, silks, sheaths, and husks, and reported simple mendelian behavior in F_1 and F_2 of certain crosses. With this exception, Gernert's extensive investigation of plant-color types has not been reported, but the writer has been able, thru an exchange of material, to compare some of Gernert's types with those in his own cultures.

SOURCE AND DESCRIPTION OF MATERIALS USED

The plant-color types discussed in this paper came in the main from the crossing of two little-known varieties, one of which was obtained at a national corn exposition and the other from an exhibit at a local agricultural fair. One of the color types produced by this cross is the same as that of the dent varieties generally grown thruout the Corn Belt; a second is not infrequently seen in certain pop, flint, and sweet corn varieties; and a third occurs in the fields of flour corn of certain Indian tribes of the Southwest. One of the color types produced by the cross had no existence, so far as the writer knows, until it appeared in his cultures. Modifications of several of the six color types noted above have been produced by crossing with a color type common in a few varieties of sweet corn and closely related to the type most common in field maize. The principal color types concerned in this account are discussed in some detail in the descriptive notes below. They are:

I — Purple
II — Sun red
III — Dilute purple
IV — Dilute sun red
V — Brown
VI — Green

PURPLE, TYPE I

Material of the purple type was first obtained as a single ear from a local agricultural fair at Nehawka, Nebraska, in 1906. The varietal name is unknown. The uncrossed stock was a smooth-seeded pop corn

of medium size. No other stock of purple has been used in the crosses described later in this account, and the writer has never seen this color type in cultivation outside his own cultures. A sample of dent corn of apparently the same color type was seen at a national corn exposition in 1909. A stock of purple was obtained from Dr. Gernert in 1914 but was not used in genetic studies. Another stock of purple was received more recently (1919) from Messrs. Collins and Kempton, the seed having come originally from Bolivia.

Seedlings of the purple type are usually indistinguishable from those of types II, III, and IV (described more fully under type IVa, page 12), altho, unlike the other types, they develop some color when grown in darkness. Half-grown plants of type I usually have the lower sheaths prominently colored, in which respect they exceed type II plants in intensity of pigmentation and are sharply differentiated from types III and IV. At the flowering stage, plants of type Ia have much purple color in nearly all parts, such as the culm, the brace roots, the leaf sheaths, the husks — even the inner ones — the cob, and the staminate inflorescence including the rachis, the spikelets, and the anthers (Plates I, 1, and V, 1). In some cases the color extends over the whole leaf, and it is always seen in the midrib. The purple pigment of type Ia develops in local darkness, as has been shown by covering various parts of growing plants with several thicknesses of heavy black paper (Plate VIII, 1). The color persists in mature plants with slight fading in the outer parts due to weathering (Plate VII, 1). The pericarp of type Ia is either colorless, red, or cherry, and the aleurone is either purple, red, or colorless. With red aleurone the anthers are reddish purple, and with cherry pericarp they are usually very dark purple, almost black (Plate I, 2 and 3).

A subtype of purple known as weak purple, or type Ib, is similar to Ia but the pigmentation is less intense, particularly in the culm and the inner husks (Plate V, 2). In early stages of growth it is often difficult to distinguish Ib from IIa. The anthers of Ib are usually deep purple, as are those of Ia, and the pericarp is the same as for Ia. Another subclass of purple, Ig, is like Ia except that the anthers are green (Plate I, 4) and the pericarp is red or colorless, never cherry. The aleurone color is the same as in Ia.

SUN RED, TYPE II

Sun red, tho not a common color type, is encountered in a few varieties of sweet corn and pop corn. It is always produced in F_2 of certain crosses, notably in purple x green.

While this type is less highly colored than Ia, it has such strong color that it is not easily distinguished from the latter in early stages of growth. At the flowering stage, type IIa is sharply differentiated from type Ia in several respects. The staminate inflorescence of IIa is lighter than that of Ia, and the anthers are deep pink instead of purple (Plate III, 1). In type IIa, pigmentation of the culm, the leaf sheaths, and the husks is limited almost wholly to parts exposed to sunlight, hence the name *sun red*. The inner husks are therefore without red color, and rarely does much color develop in any but the outer layer of husks (Plate V, 3) notwithstanding the fact that sufficient light penetrates to the inner husks to induce the development of some chlorophyll in them. A tassel inclosed in a black paper bag produces no red color in either glumes or anthers (Plate VIII, 4). Since the color of sun red plants is so largely superficial, it disappears almost wholly from mature plants thru weathering (Plate VII, 2). Sun red plants have either red or colorless, but never cherry, pericarp, and either purple, red, or colorless aleurone.

Sun red of type IIg differs from IIa merely in having green instead of pink anthers. Type IIb, known as weak sun red, differs from IIa in the lesser intensity and extent of its pigmentation. Particularly the leaf sheaths and the husks are less highly colored than in type IIa. Often the color of the husks develops in alternate dark and light bars parallel to the upper margins of the overlapping husks (Plate V, 4). Types IIb and IIg have the same pericarp and aleurone colors as IIa.

DILUTE PURPLE, TYPE III

The dilute purple type, as well as the sun red, occurs regularly in F_2 of purple x green, and most of the dilute purple material in the writer's cultures came originally from this and other crosses. It was first observed in the progeny of such crosses in 1909. Recently two stocks of this color type have been received from G. N. Collins, one obtained from the Hopi Indians of southwestern United States and the other from Bolivia.

Seedlings and young plants of type IIIa show no more color than do those of type IVa, and apparently do not develop color in darkness. As the plants approach the flowering stage, they usually show somewhat more color than do plants of type IVa, particularly at the base of the culm and in the brace roots, and sometimes in the leaf sheaths. The staminate inflorescence is usually, tho not always, somewhat more highly colored than that of type IVa. The anthers are deep purple, like those of type Ia (Plate II, 1). With red aleurone the anthers are usually reddish purple, and with cherry pericarp they are dark purple, sometimes appearing nearly black (Plate II, 2 and 3). The anther color develops fully in darkness, but the glumes are slightly if at all colored when protected from light by black paper bags (Plate VIII, 3). As the plants mature, considerable color develops in the inner husks (Plate VII, 3), on the leaf sheaths, and particularly in the culm even where it is protected from strong light by the sheaths. In some cases the culm and the sheaths ultimately become nearly as strongly pigmented as type Ia, but ordinarily the mature plant is considerably less highly colored than the purple type (Plate VII, 4). The color seen in mature plants develops well in local darkness, in which respect also type IIIa is like Ia. Dilute purple differs from purple, therefore, mainly in a less intense pigmentation and in a delayed development of pigment. The pericarp of type IIIa is either red, cherry, or colorless, and the aleurone is either purple, red, or colorless, just as in type Ia.

There exists a type of plant color which is closely related genetically to type IIIa, but which lacks red or purple color in culm, sheaths, silks, glumes, and anthers and is consequently known as *Green type IIIg* (Plate II, 4). The aleurone of this type is either purple, red, or colorless, and the pericarp is either red or colorless, never cherry. With respect to aleurone and pericarp, therefore, type IIIg is like type Ig.

DILUTE SUN RED, TYPE IV

Dilute sun red is the commonest color type of maize in cultivation. It is practically the only color type seen in the dent varieties grown in the Corn Belt of the United States, and is common in flint, flour, sweet, and pop corns. Like the sun red and the dilute purple types, it always appears in crosses of purple Ia with green VIc.

The seedlings of type IVa usually show more or less sun red pigment in the coleoptile, the leaf sheath, and the leaf margins. The young

plants ordinarily have considerable color at the base of the lower sheaths, but little or no color except green in other parts except in the margins of the leaves (Plate IX, 1). When the plants are grown on infertile soil, much bright red color develops in all parts exposed to light except the youngest leaves (Plate IX, 2). The seedlings and the very young plants are not ordinarily distinguishable from those of types Ia, IIa, and IIIa. Some time before the flowering stage, the plants of this type are sharply differentiated from those of types Ia and IIa, and are usually somewhat less highly colored than those of type IIIa. In normally grown plants, the color is confined mostly to the brace roots, and to the sheaths and the exposed parts of the culm at the base of the plants. Even at the flowering stage almost no color is seen in the upper sheaths or the upper part of the culm, and very little in the husks (Plate VI, 1). The staminate inflorescense is colored much as is that of the sun red type, tho the glumes are lighter than those of type IIa and the rachis is usually nearly devoid of color. The anthers show more or less pink, as do those of type IIa. There is much variation in the extent and intensity of pigmentation of glumes and anthers (Plate III, 2, 3, and 4), due in part to genetic differences and in part probably to environmental influences. Late in the life of the plant, type IVa usually shows some color in the outer husks and also in exposed parts of the culm. Different strains show considerable variation in this respect (Plate VI, 1 and 2). Due to the slight development of pigment and because of weathering, the dry parts of mature plants show little red color (Plate VII, 6). Light is essential to the development of color in dilute sun red, IVa, just as in sun red, IIa. The aleurone and pericarp colors of dilute sun red, IVa, are the same as those of sun red, IIa.

A wholly green type, that is, one devoid of pigment other than green in the plant parts here under consideration, is closely related genetically to type IVa and is therefore known as type IVg (Plate II, 4). Phenotypically it is the same as type IIIg. Just as in case of types Ig, II, IIIg, and IVa, the pericarp of IVg is either red or colorless, never cherry, and the aleurone is either purple, red, or colorless. Genotypic diversities in the amount of color are noted for type IVa above. The lightest types of dilute sun red show no color except mere traces of red in the staminate spikelets. This condition is found in most plants of at least two varieties of sweet corn, Black Mexican and Crosby. From these varieties there

have been isolated strains that lack even this minimum of color. These strains furnished the original stock of type IVg. In no environment as yet encountered has any red or purple plant color developed in type IVg.

BROWN, TYPE V

The brown type was first seen in 1912, when it occurred in F_2 of the cross purple Ia x green VIc. So far as the writer has been able to learn, brown plant color had not been reported previously, and he is unaware of its existence outside of his own cultures or of stocks grown from them.

Seedlings and young plants of type V are wholly green. Before the flowering period is reached, a brown pigment begins to appear in the lower sheaths. At the time of flowering, the culm, the sheaths, the husks (Plate VI, 3), and the staminate inflorescence (Plate IV, 1 and 2) are brown. The anthers are usually green. The brown color extends to the inner husks, to the culm beneath the leaf sheaths, and to the cob (Plate VII, 5). That light is not essential to the development of brown is shown further by the fact that the color appears under several thicknesses of black paper (Plate VIII, 2). It is not uncommon to find traces of purple associated with the brown in the brace roots and at the base of the inner husks (Plate VI, 3). Abnormally developed tassels, not infrequently seen on plants grown in small pots in the greenhouse, in some cases show a little purple (Plate XI). The aleurone of brown plants is always colorless, except for xenia grains, and the pericarp is either brown, brownish, or colorless, never red nor cherry. Brown pericarp color of type V corresponds to red of types I, II, III, and IV, and brownish to cherry of types I and III.

GREEN, TYPE VI

The writer's stock of the green type originated from a single ear obtained at a national corn exposition held at Omaha in 1909. The corn was exhibited from southern Missouri, where it is grown locally. It is a large dent variety, rather late in season.

Cultures of type VIc, derived from this stock, show no plant color other than green at any stage of development or under any environmental conditions to which they have as yet been subjected (Plates IV, 3, and VI, 4).

Three subclasses of type VI are recognized. One of these, VIa, is like VIc in every respect except that a slight amount of brown is sometimes seen in the outer husks and sheaths (Plate VI, 5). The second, VIb. is green except for a slight tinge of brown in the spikelets of the staminate inflorescence (Plate IV, 4). As a rule, the development of brown pigment in VIa and VIb is not sufficient to differentiate with certainty the one from the other, or either from VIc. The three subclasses, a, b, and c, are therefore usually classed together as type VI. Both VIa and VIb have been isolated from crosses involving VIc. The aleurone of all type VI plants, just as in those of type V, is colorless, except for such color as may be due to xenia. The pericarp of VIa and VIc is either brown or colorless, never brownish, while that of VIb is brown, brownish, or colorless, as in the case of type V. With brownish pericarp, type VIb usually shows unmistakable brown color in the staminate spikelets.

RELATION OF PLANT COLORS TO ENVIRONMENT

From the preceding descriptive notes and accompanying illustrations, it is clear that many of the differences separating the six major color types and their several subclasses are quantitative. Purple plants are more strongly colored than are sun red or dilute purple plants. Dilute sun red plants have less color than sun red or purple plants. Weak purple plants have less color than purple ones, but more than dilute purple ones, and weak sun reds are intermediate between sun reds and dilute sun reds. Dilute sun red plants vary, from those showing considerable color to those which, except for green, are nearly colorless. Wholly green plants are classed as subgroups of both dilute purple and dilute sun red. The subclasses of type VI differ so little with respect to color that they are ordinarily thrown together as one green type. Heterozygous brown plants are lighter than homozygous ones, and, since more than one factor pair is concerned, there is a fairly smooth gradation from the darkest to the lightest browns. Plants of types VIa and VIb, when they show any brown, differ in the parts colored. The color of the staminate inflorescence, and even of other parts, of purples, dilute purples, browns, and greens of type VIb is darker when the pericarp is cherry or brownish than when it is red, brown, or colorless.

The natural intergrading of genetic types in this somewhat complex series is often made still more confusing by the variations accompanying

environmental diversities. A prominent geneticist, on observing some of the writer's cultures, was led to say that there were no sharply differentiating characteristics by which other than an arbitrary classification could be made, and asserted that he could select from a single progeny a series grading from the darkest to the lightest colors. The writer has some doubt that this could have been done, but the instance illustrates well the difficulties that confront one unacquainted with the materials. It is fortunate that some environmental influences which increase the difficulty of assorting certain color types make other types stand out more sharply than they otherwise would. Without some notion of these environmental effects, a genetic analysis of the material would indeed be difficult.

SUNLIGHT A FACTOR IN COLOR DEVELOPMENT

The relation of sunlight to the development of color has been noted briefly in the descriptions of some of the color types. The effects of sunlight or of local darkness, instead of adding to the confusion of color types, afford a means of sharp differentiation between certain types. So far as is known at present, no color develops in sun red or dilute sun red plants, or in the early stages of growth of dilute purple plants, except under the influence of fairly strong light. In the case of purple and of the later stages of growth of dilute purple, there is no doubt that the color develops more rapidly at first in light than in darkness, but ultimately color develops fully, or apparently so, even in local darkness (Plate VIII). The seedlings of purple plants develop some color when germinated and grown in a dark chamber where no part of the plant receives light. There is some, tho very little, evidence that the development of brown pigment of type V is hastened by the influence of light, and what little brown color ever develops in type VIa is confined to parts exposed to sunlight (Plate VI, 5).

It would not be surprising to find that the pigments seen in the purple, dilute purple, sun red, and dilute sun red types are the same chemically. In fact they look alike in water solution and apparently react in the same way to simple chemical tests. If they prove to be identical, it would seem to follow that purple and dilute purple plants have some inherent mechanism, perhaps an organic catalyzer, capable of initiating or hastening chemical reactions, and that this mechanism is lacking in sun red

and dilute sun red plants, in which the same reactions may possibly be brought about thru the action of sunlight.

Usually a single thickness of black paper, such as is employed to protect photographic plates from light, is sufficient to prevent the development of color in sun red plants (Plate VIII, 4). That more intense light is necessary for the production of sun red pigment than for the production of chlorophyll is shown by the almost entire absence of red color in all but the outer husks, while even the innermost husks are somewhat green (Plate V, 3). The pigments of purple and brown plants, on the contrary, develop well even when there is too little light for the formation of chlorophyll (Plate VIII, 1 and 2).

That the effect of light on color development is a definitely local one is shown by the sharp line of demarcation between colored and colorless areas in culms, husks, and sheaths partly exposed and partly protected by overlapping sheaths or husks (Plate V, 3). Even a single piece of wrapping cord tied closely about a young ear, sheath, or culm of a sun red plant is sufficient to prevent the development of color beneath it. Evidently sun red pigment does not diffuse appreciably from the cells in which it forms. It is not meant to suggest by these observations that sunlight has no effect other than a local one on color development. On the contrary, there is evidence that the development of sun red color is influenced by the presence of an abundance of carbohydrates which in turn are dependent on sunlight for their formation.

A striking example of the relation of sunlight to color development is afforded by the barred pattern seen in the husks of some weak sun red plants (Plate V, 4). The pattern consists of alternate bars of red and green parallel to the upper margin of the overlapping husk next below them. By tracing in pencil on each exposed husk of a rapidly growing ear the margin of the husk overlapping it, it has been ascertained with certainty that the red bars correspond to the areas that are pushed out from under the overlapping husk between early morning and late afternoon, while the green bars correspond to the areas pushed out during the late afternoon and night. Why color develops in only those parts of the husk that receive the sunlight when first exposed to the air, and not in the parts exposed some hours previously, is not known. Another illustration of the effect of sunlight on freshly exposed husks was seen in a very light type of weak sun red (Plate V, 5). Of two ears on the same culm, both very lightly

and about equally colored, the lower had its husks torn apart in the early forenoon so that the fresh inner husks were exposed at once to direct sunlight. In a few hours some red color began to show, and in a few days all the newly exposed husks were brilliantly colored, while the undisturbed upper ear remained only slightly colored. Similar results followed in repeated trials, and, in fact, failed only when the atmospheric conditions were such as to cause the newly exposed husks to wither during the first day. It is of interest to note also that similarly treated ears of dilute sun red plants, which rarely show any red color in the outer husks of young ears, failed to develop color when the husks were torn apart, even tho they remained fresh for some days.

It is evident from all this, that, with respect to their relation to sunlight, there exists a series of color types varying more or less abruptly from dilute sun red, in which little or no sun red develops in even freshly exposed husks, thru weak sun red, in which color forms in only freshly exposed husks, and strong sun red, in which much color develops in all exposed parts of the husks but not in parts protected from light, to strong purple, in which, tho sunlight may hasten color development, it is not essential to its formation.

Tests of the influence on color development of light of different wave lengths have not been uniformly successful. Cramer photographic color screens were placed in partial contact with the uncolored inner husks of sun red plants, and the entrance of light otherwise than thru the screens was prevented by means of strips of black paper. These screens, by cutting out light of certain wave lengths, not only change the quality of light passing thru them but lessen the intensity of the light. While the results, therefore, can have little value, it may be of interest to physiologists to note that considerable sun red formed under the orange and the bright red screens, and little or none under the green and the blue screens.

MOISTURE IN RELATION TO COLOR

It is well known that under field conditions maize does not grow well in wet soil. In such situations, not only are the plants small, with their leaves pale green, but they often develop much red pigment. The writer has repeatedly observed that young plants, in flooded parts of fields where the soil had been covered with water for some days, were brilliantly red in all parts except the youngest leaves, while near-by plants on slightly

higher land showed only the slight red at the base of the culms characteristic of young dilute sun red plants.

For a study of the effect of soil moisture on color development under controlled conditions, plants of well-known stocks of purple Ia, sun red IIa, dilute purple IIIa, dilute sun red IVa, brown V, and green VIc and IVg, were grown in rich soil in earthen jars in the greenhouse during the summer of 1914. When the plants had reached a height of from 10 to 15 centimeters, the jars were separated into three lots — one with dry soil, another with moist soil, and a third with wet soil. The dry-soil lot received only sufficient water to keep the plants growing slowly and not enough to prevent wilting during the hotter part of the day. The moist-soil lot received just sufficient water to insure normal growth. The wet-soil lot was kept constantly in saturated soil with some free water above the soil surface. The test was continued until the plants of all lots reached the flowering stage.

The plants in moist soil made the most rapid growth and flowered somewhat earlier than the plants of the other lots. Their leaves were of normal green color and they showed the colors characteristic of the several color types. The plants in dry soil were smaller and very dark green. The development of purple, red, and brown color was practically the same as with the plants in moist soil. The plants in wet soil grew less rapidly than those in moist soil, but more rapidly than those in dry soil. Their leaves were somewhat lighter green than those of the moist-soil lot, but they showed practically the same amount of purple, red, and brown color. In fact the only differences between the three lots with respect to color at any time during the test were such as might well be related to the stage of development of the plants. All color types show more color in the later stages of growth. The moist-soil lot developed somewhat more rapidly than did the others and for a time showed slightly more color, but ultimately all lots had practically the same amount of color. Evidently the reddening of plants in flooded fields is not due directly to the excess of soil moisture.

TEMPERATURE IN RELATION TO COLOR

Since moisture is not the direct cause of the reddening of maize plants in flooded fields, tho certainly connected with the phenomenon in some way, it follows that the effect must be produced by some indirect action

of the excess of water. Wet soils in spring are cold soils, and if the wet areas are of considerable extent the air above them is doubtless somewhat cooler than that above drier soil. It has been frequently observed that young plants which show much color during a cold spring show considerably less in the leaves developed after the weather has become warmer. Young plants of early-planted maize sometimes have more color than plants that are started later. Moreover, full-grown plants from late plantings often develop more color in the cool weather of autumn than similar plants that mature in the warm weather of late summer. It seemed important, therefore, to study the effects of various temperatures on color development.

The same color types and the same stocks—in one test the identical plants—used in the soil-moisture test were grown in the greenhouse under diverse temperatures. Altho both rich and poor soils of diverse water content were used, the comparisons noted here were made between plants in the same kind of soil and with practically the same soil-moisture conditions. Two lots were grown during the winter of 1913-14 and two during the following summer. During the winter, one lot was kept in a warm house at temperatures varying from about 18° to 26° C., and one was kept in a cool house at temperatures varying normally from about 7° to 15° C. but during a part of the test dropping at night to 1° or 2° C. Both lots were exposed to the full winter sunlight of the houses. During the summer test, one lot was kept as cool as possible by partial shading and free ventilation, the temperatures ranging from about 15° to 40° C. but occasionally exceeding these limits, and the other lot was kept in an unshaded house the ventilators of which were never opened. The night temperatures of the closed house averaged not more than one degree higher than those of the open house, but the maximum day temperatures in the closed house varied usually from about 44° to 50° C. and on three consecutive days reached 55° C. This extreme heat killed most of the plants grown in rich soil but did not seriously injure those in poor soil. Of course the relative humidity, as well as the intensity of the light, was materially different for the closed and the open house.

As a result of these tests, no final differences in the development of color in any of the color types were observed between the lots grown at the very diverse temperatures. Of course differences were observed at certain times, but they are readily accounted for by the facts that the

plants developed less rapidly at both excessively high and excessively low temperatures than at more moderate temperatures, and that color shows less during the early stages of development than during later stages. It may be safely concluded, therefore, that color development in maize is not notably influenced, except perhaps indirectly, by diverse temperatures.

SOIL FERTILITY AND COLOR DEVELOPMENT

There is still another way in which it was thought the excess of water might indirectly affect the development of color in maize plants in flooded fields. Not only may nutrient salts be removed in part by an excess of water, but certain of these salts — nitrates — are not formed normally in very wet soils. Tests were made, therefore, of the relation of soil fertility to color development.

Rich compared with poor soil

The same plant-color types as were employed in the soil-moisture and temperature tests were included in these soil-fertility tests. In fact, for one of the tests the same plants were used as in the moisture and temperature studies. One lot of plants was grown in rich soil and a duplicate lot in poor soil. Field soil furnished the basis of both soils. To one lot was added about 50 per cent by measure of thoroly decayed stable manure, and to the other about 50 per cent of clean sand.

The effect of soil fertility on color development of certain color types was strikingly apparent from the time the seedlings were two or three weeks old. At this age and for some time later, there was no appreciable difference in color between purples, sun reds, dilute purples, and dilute sun reds. In the rich soil all these color types had very little red color. There was some color in the coleoptile and the lower leaf sheath, but none in the leaf blades except for a slight amount in their margins. The same color types in poor soil had considerable color in the leaf blades and much color in the leaf sheaths. The plants in rich soil grew rapidly and were dark green, even the lower leaves remaining healthy. The plants in poor soil, on the contrary, grew less rapidly and were lighter green, and their lower leaves soon became yellow and died. In all cases the leaf blades became brilliantly red before they died. This is in strong contrast with the condition of the lower leaves of plants in dry, rich soil. When the

death of the lower leaves is caused by drouth, there is no corresponding development of red color.

At the age of six weeks, the plants in rich soil were beginning to show slightly the color differences that in later stages are characteristic of purples, sun reds, dilute purples, and dilute sun reds. In poor soil, on the contrary, no color differences were seen. All the four types were highly colored thruout except for the youngest leaves (Plate IX, 1 and 2).

At the flowering period, the plants in rich soil exhibited all the peculiarities of color by which purples, sun reds, dilute purples, and dilute sun reds are normally differentiated. Even in the poor soil something of the same color differences were discernible between the purples and sun reds on the one hand and the dilute purples and dilute sun reds on the other, but it is doubtful whether these two groups could have been separated accurately from a mixed culture. It would have been very difficult also to separate with certainty the purples from the sun reds or the dilute purples from the dilute sun reds, except by differences in anther color and by an examination of the inner husks and other parts protected from sunlight. Differences between the plants in rich and in poor soil were still pronounced in the case of dilute purples and dilute sun reds, but were scarcely discernible in the case of purples and sun reds except that the leaf blades were somewhat more highly colored with poor than with rich soil and that thruout the plants the colors appeared brighter in the former case owing to the less intense green of the poor-soil lots.

The seedlings of both brown and green color types showed no brown nor red color in either the rich or the poor soil. At the age of two months, some brown pigment began to show in the lower sheaths of the brown type, and at the flowering stage the plants had the typical coloration of brown plants. The difference in the development of brown between rich and poor soil was at no time very noticeable. The color showed perhaps slightly earlier, and was perhaps slightly more intense, with the poor soil. Even this apparent difference, however, may have been due merely to the fact that the plants in poor soil were lighter and more yellowish green than those in rich soil. Dark green might readily mask the brown color somewhat. Green plants of both type VIc and type IVg exhibited no red nor brown color at any stage of development in either rich soil or poor soil.

From these observations it is apparent that variations in soil fertility may effectively obscure genetic differences. A knowledge of the influence of soil fertility on color development is therefore essential to careful genetic work with the plant colors of maize. Moreover, since soil fertility is subject to control thru cultural methods, different degrees of fertility can be used as an aid to the sharp differentiation of certain genetic types. If, for instance, it is desired to separate, in the seedling stage, greens and browns on the one hand from the red-purple series on the other, this can be accomplished most readily in poor soil. In fact, the writer's practice, in studies requiring this separation, is to grow the seedlings in pure sand. In this medium seedlings of the purple-red series of color types become highly colored at a very early age, while seedlings of the green and brown types show absolutely no red color. If, however, it is desired to distinguish sharply between purple and dilute purple or between sun red and dilute sun red, fairly fertile soil is essential, and, usually, the more fertile it is, the more easily can the separation be made. The stronger colors develop almost as well in rich as in poor soil, while the weaker colors develop much less intensely in rich soils than in poor ones. On very poor soils, it is difficult to separate sun reds from dilute sun reds, and almost if not quite impossible to distinguish with certainty between sun reds and weak sun reds or between weak sun reds and dilute sun reds.

Lack of particular nutrient elements

It having been established that differences in soil fertility result in marked differences in the development of red color in maize plants, it seemed important to determine whether particular nutrient salts are more concerned than others. Accordingly, plants of all the color types included in the tests previously reported were grown in glazed earthen jars in clean quartz sand and watered with nutrient solutions. The quartz sand was obtained from the Department of Agronomy of the University of Nebraska, and was known to be practically free from nutrient elements except iron. The nutrient salts and distilled water were obtained from the Department of Agricultural Chemistry of the same institution. The nutrient solution employed was one that had given good results with maize in certain experiments conducted previously by the Department of Agronomy. The complete nutrient solution, 0.2 per cent strength, contained per liter of water the following salts: 1 gram $Ca(NO_3)_2$, 0.25

gram KNO_3, 0.25 gram K_2HPO_4, 0.25 gram $MgSO_4$, and 0.25 gram NaCl. Other solutions of approximately equivalent molecular strength, but each lacking one of the nutrient elements of the complete solution, were used. In the nitrogen-free solution, 0.7 gram $CaCl_2$ and 0.22 gram K_2SO_4 were substituted for $Ca(NO_3)_2$ and KNO_3, respectively; in the phosphorus-free solution, 0.25 gram K_2SO_4 for K_2HPO_4; in the potassium-free solution, 0.2 gram $NaNO_3$ and 0.2 gram Na_2HPO_4 for KNO_3 and K_2HPO_4, respectively; in the calcium-free solution, 1 gram $NaNO_3$ for $Ca(NO_3)_2$; in the magnesium-free solution, 0.3 gram Na_2SO_4 for $MgSO_4$; and in the sulfur-free solution, 0.2 gram $MgCl_2$ for $MgSO_4$. A complete nutrient solution of four times the strength indicated above, 0.8 per cent, was also used, and one lot was given water without the addition of nutrients. After the first three weeks, the nutrient solutions were all used at double strength, 0.4 and 1.6 per cent, and clear water was occasionally given. This treatment, owing to considerable evaporation of water, doubtless resulted in a gradual increase in the strength of the solutions. The tests were carried on at the same time with one of the tests of rich and poor soil, so that the latter might serve as a check on the nutrient-solution tests.

At first the seedlings given 0.2-per-cent complete nutrient solution reacted about as did those in poor soil, while those given 0.8-per-cent nutrient solution were no more highly colored than those in rich soil. At one month of age, the plants watered for three weeks with 0.2-per-cent and one week with 0.4-per-cent complete solution were growing rapidly and were no more highly colored than those in rich soil, while the plants in the very strong solutions (0.8 and 1.6 per cent) were beginning to wilt, perhaps from the toxic effect of the solutions. Thruout the remainder of the test, the plants given 0.4-per cent solution, alternated occasionally with clear water, were practically like those growing in rich soil both as respects vigor of growth and color development.

In striking contrast to the plants given complete nutrient solution were the ones given clear water and those in nitrogen-free nutrient solution. Both these lots showed much color even at two weeks after germination, and soon thereafter the seedlings were red to the tips of their leaves. At the age of six weeks the plants of these two lots were much shorter and slenderer than those given complete nutrient solution. Their upper leaves were pale yellowish green, with much red, and the lower leaves were dead but still showing the red color that had developed earlier.

Next in point of coloration to the seedlings given nitrogen-free nutrient solution and those given water alone, were the ones grown in phosphorus-free nutrient solution. The latter did not show red color so quickly as did the nitrogen-free lot, and at no time did they develop quite so much color. They showed, however, considerably more color at the age of one month than did seedlings in the complete nutrient solution. When six weeks old the plants of the phosphorus-free lot were relatively small, and had pale green upper leaves with little red color and dead lower leaves which still retained much red pigment. While somewhat larger than the plants in nitrogen-free solution and those in clear water, the phosphorus-free lot began wilting when about six weeks old and died considerably in advance of the nitrogen-free lot. Their roots showed early indications of injury, perhaps from toxic effects of the solution.

Plants of all the other lots, in which one or another nutrient element had been omitted from the solution, exhibited little or no color reaction to the lack of a particular element. All of them were more vigorous in growth than the nitrogen-free and phosphorus-free lots, but much less so than the lot given complete nutrient solution. The sulfur-free lot for a time seemed to be developing more red, but later showed perhaps even less red, than the lot with complete nutrient solution. The magnesium-free lot showed prominent dark and light green stripes in the leaves similar to the green-striped chlorophyll pattern (Lindstrom, 1918). In some cases the tissue of the lighter stripes died and there was often some red coloration next to the dead tissue. The potassium-free lot had about the same amount of red color as the lot given complete nutrient solution, while the calcium-free lot showed less red color than any other lot in the test.

It is perhaps noteworthy that in the nitrogen-free lot, and to some extent in the phosphorus-free lot, the new growth seemed to take place at the expense of the older leaves. The lower leaves first became light or yellowish green, then red, and finally died. That the development of red pigment is not necessarily connected, however, with the breaking down of the protoplasm, is seen in the failure of seedlings to develop red color in the older dying leaves of the lot in complete nutrient solution and of the potassium-free, magnesium-free, and calcium-free lots. In the calcium-free lot, growth was stopped by the death of the youngest parts, including the partly unrolled upper leaves, and yet these parts showed

no red. Moreover, the dying of the lower leaves due to excessively dry soil, or of the upper leaves from intense heat, is not accompanied by the development of red pigment.

In similar tests with cuttings of *Tradescantia viridis* and *T. lockensis* grown in distilled water, in complete nutrient solutions, and in solutions each lacking one nutrient element, namely, N, P, K, Ca, Mg or S, Czartkowski (1914) found that after five weeks red color appeared in the newly developed leaves in the cases of only distilled water and nitrogen-free solutions. He states, however, that Susuki reported a similar effect on plants of Hordeum from a lack of phosphorus. It will be recalled that in the writer's tests with maize, lack of nitrogen gave the most pronounced effect and lack of phosphorus induced considerable color development, while lack of sulfur seemed for a time to have an effect but no effect was apparent later.

From the results of the tests reported above, it is apparent that the reddening of young plants in flooded fields, as well as the intensification of color in older plants grown on poorly drained heavy soils, is not due to any direct effect of the excess of water in the soil or to a direct effect of the somewhat lower temperatures accompanying such conditions, but rather, perhaps, to the lessened fertility of cold, wet soils or to inability of the plant to obtain adequate nutrients under such conditions. An excess of water not only may remove certain nutrient salts from the soil, but also may prevent or greatly check nitrification. Moreover, under these conditions the soil solution is probably less concentrated. The reddening of young plants in cold, wet soils in spring, the greater development of color in plants maturing in the cool weather of late autumn, and the excessive development of red in plants on very light sandy soils, are possibly all due to the plants' inability to get from such soils an adequate supply of nutrient salts, particularly of nitrates.

RELATION OF CARBOHYDRATES TO COLOR

Several authors, notably Wheldale (1911), have discussed the relation of sugars to the production of anthocyanins in plants. Knudson (1916: 24, 62) found that maize and vetch grown in nutrient solutions containing certain sugars developed markedly more red color than did plants grown in sugar-free solutions. The writer has observed repeatedly an apparent relation between an excess of carbohydrates and the development of red

color in maize leaves. Of course the relation has been observed only in types that normally produce some red pigment. Neither brown, type V, nor green of either type IVg or type VI, has ever been observed with red color in the leaves, no matter what treatment has been given the plants. When leaves are folded at right angles to the midrib and the margin of the fold is creased sufficiently to break the softer tissues but not enough to break the water-conducting vessels, the part beyond the crease does not wilt, but within a few days it begins to lose some of its chlorophyll and within a week it becomes highly colored red (Plate X, 1). When leaves are similarly treated late in the afternoon of a bright day and the plants are kept in a dark room until the following day, the starch is, of course, found to have disappeared by translocation from the part of the leaves below the crease, while the cells of the bundle sheaths of the part beyond the crease are found to be packed with starch. There is so much starch in this part of a creased leaf that, on extraction of the chlorophyll with alcohol and treatment with iodin, the whole end of the leaf becomes almost black. While this does not prove a direct relation between an excess of carbohydrates and the development of red pigment, taken in connection with all the other observations it strongly suggests such a relation.

It has been observed repeatedly that sweet-corn plants from which the ears have been removed in the edible stage develop within a week or two much more color than do neighboring plants that still retain their ears. Barren stalks also frequently show more color than do their ear-bearing neighbors. While no direct determination of the matter has been made it seems likely that barren plants, as well as plants from which the immature ears have been removed, may carry, in their leaves, husks, and culms, an excess of carbohydrates which would normally have been deposited in the developing seeds.

The strong development of red pigment in the white, chlorophyll-free stripes of the japonica-striped type, when leaves are creased or when plants are grown in poor soil, may well be due to the passage of sugars from the green to the white parts. In some instances the red color seems to develop more quickly in the white stripes than in the green (Plate X, 2). Whether this difference is a real one, due perhaps to the readier access of light to the white parts, or is only an apparent difference due to the

masking effect of the green color, is not known. Certainly red pigments develop first in the chlorophyll-free epidermal cells.[2]

Czartkowski (1914) suggested, in connection with the account of his study of the relation of nutrient elements to color development, that lack of nitrogen may check protein synthesis, thus leaving unused the carbohydrates that would otherwise be used in growth, and that the excess of carbohydrates may favor anthocyanin formation. He was unable to understand why a lack of phosphorus or of sulfur did not likewise influence color development, since these elements also are necessary to protein synthesis. Lack of phosphorus does apparently bear some relation to color development in maize, but the writer's tests afforded little or no evidence of such a relation between a lack of sulfur and pigment formation. If lack of nitrogen induces anthocyanin formation thru the checking of growth, thus allowing an accumulation of carbohydrates, it is not clear why other means of checking growth, such, for instance, as dry soil, do not also favor pigment formation, unless these other growth-checking factors at the same time limit photosynthetic activity. It is of interest to recall in this connection that plant colors of maize — brown no less than the red-purple series — develop first in the older parts where growth first ceases, such as the lower sheaths and the upper parts of the internodes of the culm.

SUMMARY

Whatever is the final outcome of studies of the relation of environmental factors to plant-color development in maize, enough has been noted to indicate a very complex relation. What is more complex than this chain of events — a chain that lacks many links in the way of particular chemical reactions: cold, wet soil checks or inhibits nitrification; lack of nitrogen in available form limits protein synthesis, which in turn allows an accumulation of carbohydrates; an excess of carbohydrates favors anthocyanin formation. The result is that young maize plants in cold, wet soil become highly colored. But to all this must be added the factor of sunlight, without which no red color develops in the leaves of young plants. And not the least consideration is the important fact that only plants of certain genetic constitutions show this color reaction to wet soils. It is to be hoped that some day, thru the coordinated efforts of

[2] The histology of color development of the several plant-color types has been investigated by Dr. E. G. Anderson, but the observations have not been published.

biochemists, physiologists, and geneticists, it may be possible to reach conclusions in this field of quite as fundamental importance to biology as the recent results of similar efforts of cytologists and geneticists.

GENETIC ANALYSIS OF COLOR TYPES

In the preceding parts of this paper the several plant-color types of maize are described and the variations induced in them by diversities of environment are discussed. The remainder of the paper is devoted to a presentation of data of a more distinctly genetic nature, and to an attempt at a factorial analysis of these data.

The data are presented as if the F_2 generation of the more complex crosses were the first which were obtained and on which hypotheses were formulated and appropriate tests made. As a matter of fact, this was not in all cases the actual procedure. In several instances the results of some of the simpler crosses were at hand and were used as an aid to the interpretation of the more complex ones when the latter were obtained. Moreover, the hypothesis presented here was not the only one, nor indeed the first one, formulated. As is usual in such work, various hypotheses were devised, tested, and discarded, until finally a factorial interpretation was found that fitted fairly well all the facts known. Many results with a bearing on plant color were obtained in other studies extending over a period of some eight or nine years. Since the practice of the writer is to number his pedigrees consecutively from year to year, an inspection of the pedigree numbers, as listed in the tables, suggests at once that some of the data presented as checks on other results could not have been obtained after these other results. Any data applicable as a test have been so used whether obtained for that purpose or in connection with other studies. Whether this mode of presentation is the best one must be left to the judgment of others. This at any rate is certain: the data could not have been presented chronologically and discussed in relation to such hypotheses as happened to be under test at the time any particular results were obtained, without adding unnecessarily to the complexity of the paper.

CROSSES INVOLVING THE FACTOR PAIRS *A a*, *B b*, *Pl pl*

Purple Ia x green VIc

Generations F_1 and F_2.— When purple plants with purple anthers (type Ia) are crossed with plants lacking all red, purple, or brown

pigment, commonly known as green (type VIc), the F_1 offspring are full purple. Whether or not a quantitative determination of purple pigment might reveal a difference, no dilution of the purple color is apparent to the eye in the F_1 plants. Four crosses of this sort with a total F_1 progeny of 111 purple plants are listed in table 1 (appendix, page 121).

Seven F_2 progenies of the F_1 plants recorded in table 1 are listed in group 1 of table 2. Fourteen other similar F_2 progenies are shown in group 2 of the same table. The F_1 plants from which these fourteen F_2 progenies came are not recorded in table 1 because their purple parents were not homozygous. Some of the purple plants used as parents in these crosses were F_1's of the original cross of purple with green. Others were from F_1 or some later generation of other crosses having the purple type as one parent. In every case the other parent was a green plant of type VIc. Since the purple F_1 plants of these crosses were presumably the same genotypically as the F_1's shown in table 1, their F_2 progenies may well be included tentatively with those of group 1 of table 2. Each of the twenty-one F_2 lots exhibited six distinct classes of plants with respect to color. The 2117 plants were distributed among the six classes as follows:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
952	305	275	91	278	216	2,117

Obviously no simple 3:1 mendelian behavior is in evidence here. Moreover, only four classes are expected in dihybrids where dominance is exhibited. With dominance trihybrids ordinarily give eight classes in F_2 in the well-known numerical relation of 27:9:9:3:9:3:3:1, while only six classes were observed. Inspection of the distribution of the 2117 individuals given above, however, suggests the possibility of a 27:9:9:3:9:7 relation, which should be realized in a trihybrid if the last three classes were indistinguishable. A comparison of observed numbers with those expected on this hypothesis follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed........	952	305	275	91	278	216	2,117
Calculated[3]......	893	298	298	99	298	232	2,118
Difference.......	+59	+7	—23	—8	—20	—16	—1

[3] In this and most of the following comparisons, the theoretical distributions are calculated to the nearest whole number.

There are rather large differences between observed and expected numbers. The purples are considerably, and the sun reds slightly, in excess of expectation, while each of the other four classes has too few individuals. The probability that these deviations may be due to chance is approximately 0.11. One might expect, therefore, to encounter chance deviations of the magnitude observed here about once in nine such trials. This, of course, does not substantiate the three-factor hypothesis, but merely indicates that it is not necessarily out of keeping with the observed facts.

Backcrosses with green VIc.— A better criterion perhaps is afforded by the backcross of F_1 purples with the green parent type. Records of such crosses are shown in table 3. The backcrosses with F_1's of table 1 are listed in group 1, and backcrosses with similar F_1 purples of other lots in group 2. The same six phenotypes observed in the regular F_2 generation occurred here also. On the basis of the three-factor hypothesis and with the assumption that there are three sorts of greens indistinguishable from one another, the individuals of this backcross should be distributed equally to five classes with the sixth class containing three times as many individuals as any other class. The observed distribution of the 1317 individuals of the fourteen progenies is here compared with the expected distribution:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed........	170	160	176	160	172	479	1,317
Calculated.......	165	165	165	165	165	495	1,320
Difference.......	+5	—5	+11	—5	+7	—16	—3

While a few of the backcross progenies listed in table 3 exhibit considerable deviations from the expected distribution, the fourteen lots taken together approximate it closely. The probability that the observed deviations may be due to chance in random sampling is about 0.85. Deviations as great as these are to be expected thru chance alone, therefore, in about six out of seven trials.

Working hypothesis.— To the three factor pairs used to interpret the results here reported, the symbols *A a*, *B b*, and *Pl pl* have been assigned. The gene *A* is an anthocyanin factor. In the presence of *a a* ordinarily no anthocyanic pigment develops, tho brownish, or flavonol (Sando and Bartlett, 1921), pigment may be formed. The pair *B b* is named for its

connection with the development of brown pigment, tho when both *A* and *B* are present, sun red pigment is produced. The pair *Pl pl* is so termed because of its relation to purple pigment. The phenotypic formulae assigned to the several classes of plant color under consideration here are as follows:

A B Pl —	Ia,	purple
A B pl —	IIa,	sun red
A b Pl —	IIIa,	dilute purple
A b pl —	IVa,	dilute sun red
a B Pl —	V,	brown
a B pl —	VIa	green
a b Pl —	VIb	green
a b pl —	VIc	green

Obviously the hypothesis in accordance with which the above factorial assignments have been made is subject to several genetic tests. Naturally the first tests to suggest themselves are studies of the behavior of the several F_2 types in F_3 and later generations. Next in order are intercrosses between the several classes. For reasons that will appear shortly, one of these intercrosses is here dealt with before consideration is given to F_3 generations from the several F_2 classes.

Dilute sun red IVa x brown V

From an examination of the factorial assignments listed above, it is evident that crosses of dilute sun red, *A b pl*, with brown, *a B Pl*, should produce purple F_1 plants, *A B Pl*. Moreover, these F_1 purples should be heterozygous for all three factors, *A a B b Pl pl*, just as was assumed for the original cross of purple, *A B Pl*, with green, *a b pl*. The F_2 and later behavior of this cross should also, barring linkage, be like that of the original cross, so that the two can most conveniently be considered together.

Generations F_1 and F_2.— The F_1 generation of twenty-six crosses of dilute sun red with brown plants is given in table 4 (page 123). The dilute sun red parent plants were chosen from any convenient lots known to be homozygous with respect to *A*, *b*, and *pl*. The brown parent plants, on the other hand, were from the F_2 and later generations of the original cross of purple and green or from other crosses. It was to be expected, therefore, that some of the brown plants would be homozygous for both *B* and *Pl*, and some would be heterozygous for *B*, some for *Pl*, and some

for both *B* and *Pl*. This expectation was fully realized. In group 1 of table 4 are recorded the progenies of nine crosses with a total of 263 individuals. All but one plant of the lot were purple. The one dilute sun red plant was presumably due to accidental pollination of the dilute sun red mother plant. Since the dilute sun red parents of all these crosses were *A A b b pl pl*, the brown parents of the crosses listed in group 1 must presumably have been *a a B B Pl Pl*. Similarly, the seven crosses listed in group 2 gave purple and sun red plants only, 143 of the former and 147 of the latter. Evidently the brown parents of these crosses were *a a B B Pl pl*. Again, the six crosses shown in group 3 gave 105 purple, 123 dilute purple, and no other plants. The brown parents of the crosses were therefore, presumably, *a a B b Pl Pl*. Finally, the four crosses listed in group 4 gave 9 purple, 11 sun red, 19 dilute purple, and 17 dilute sun red. The brown parents of these four crosses are assumed, consequently, to have been *a a B b Pl pl*.

The F_2 results from the purple F_1 plants of these crosses of dilute sun red with brown are recorded in table 5. Fourteen progenies of the F_1 plants listed in table 4 are shown in group 1 of table 5, and five progenies from similar F_1 plants not listed in table 4 are entered in group 2. Here, just as with the results of the cross of purple with green (table 2), fairly marked discrepancies between theory and observation appear when the several progenies are taken separately. When, however, the nineteen progenies are considered together, very close agreement is found between observation and expectation, as is shown by the comparison below. The probability that such deviations as are observed may be due to chance is approximately 0.88, which means that only about once in eight trials would as good a fit be expected. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed.....	847	282	281	94	267	233	2,004
Calculated....	845	282	282	94	282	219	2,004
Difference....	+2	0	—1	0	—15	+14	0

Backcrosses with green VIc.— In addition to the F_2 results noted above as derived from self-pollinated F_1 purple plants, a few F_1 purples were back-

crossed with the triple recessive green, type VIc. The records of these crosses, seven in all, are presented in table 6. The results are, as expected, in close agreement with the backcross data from the cross of purple with green. The comparison below indicates a good fit of calculated to observed frequencies for the lot as a whole. The probability that such deviations as are observed may be due to mere chance is about 0.82, indicating that as great departures from expectation as these might be expected about four times in five trials. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed....	84	72	78	72	79	249	634
Calculated....	79	79	79	79	79	237	632
Difference....	+5	—7	—1	—7	0	+12	+2

Backcrosses of Ia x VIc and IVa x V with IVa

Purple plants of F_1 of the crosses purple x green and dilute sun red x brown were crossed with homozygous dilute sun red stocks. On the basis of the hypothesis used above, the F_1 plants are assumed to be *A a B b Pl pl* and the dilute sun red plants *A A b b pl pl*. Four classes of plants, purple, sun red, dilute purple, and dilute sun red, should be produced in equal numbers by this cross. The data are presented in table 7 (page 125). Progenies of F_1 plants from the cross purple x green are listed in group 1 and those from the cross dilute sun red x brown in group 2. As will be seen from the comparison below, the observed numbers are in fair agreement with the hypothesis. The probability that such deviations as occur may be due to chance is approximately 0.67. In other words, there are two chances in three that deviations of this sort are due to errors of random sampling alone. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed...............	299	270	288	291	1,148
Calculated.............	287	287	287	287	1,148
Difference.............	+12	—17	+1	+4	0

Behavior of F_2 color types in later generations

From all the foregoing it appears that the results obtained are in close accord with the proposed three-factor hypothesis in the case of both the cross purple x green and the cross dilute sun red x brown, and not alone for the F_1 and F_2 generations but also for backcrosses with green and with dilute sun red. It is now in order to inquire into the behavior of these crosses in F_3 and later generations. In the presentation of the additional data, the two crosses purple x green and dilute sun red x brown will be considered together.

Later behavior of F_2 purple Ia.— Purple plants of the F_2 generation of the crosses under consideration are expected to be of eight genotypes. The expected F_2 genetic formulae and the F_3 color classes, together with the relative numbers of each, are as follows:

F_2 genotypes	F_3 color types					
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VI
1 — *A A B B Pl Pl*............	1	......	......	......	......	......
2 — *A A B B Pl pl*............	3	1	......	......	......	......
2 — *A A B b Pl Pl*............	3	......	1	......	......	......
2 — *A a B B Pl Pl*............	3	......	......	......	1	......
4 — *A A B b Pl pl*............	9	3	3	1	......	......
4 — *A a B B Pl pl*............	9	3	......	......	3	1
4 — *A a B b Pl Pl*............	9	......	3	......	3	1
8 — *A a B b Pl pl*............	27	9	9	3	9	7

If, instead of being selfed, the F_2 purple plants are backcrossed to green of type VIc, the same F_3 color classes are expected but the several classes should, of course, be equally frequent except in case of the F_2 triple heterozygotes, which should throw three times as many greens as of each of the other five types.

The F_3 data from thirty-five F_2 plants are recorded in table 8 (page 125). In group 1 of the table are listed the progenies of eight selfed and one backcrossed F_2 plants. From the backcross six color types appeared in frequencies of 4:4:11:4:4:18. The theoretical number for the first

five classes is 5.6 and for the sixth class is 17. The probability that such deviations as occur are due to chance is approximately 0.35, or more than one in three. The eight self-pollinated plants gave together the six types in frequencies as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VIa, b, c	
Observed......	193	66	60	16	57	34	426
Calculated.....	180	60	60	20	60	46	426
Difference.....	+13	+6	0	—4	—3	—12	0

The probability that such deviations as occur may be due to errors of random sampling is practically 0.27. Similar deviations might therefore be expected somewhat more than once in four trials. It will be noted that two progenies lacking class IV are included in this lot (group 1, table 8). The total number of plants in these progenies were 37 and 17, respectively, and they should therefore have had, respectively, two and one plants in class IV.

Five F_2 purple plants (group 2, table 8) gave four color types (Ia, IIa, IIIa, and IVa) in F_3, with total frequencies as shown below. Here the probability, P, equals 0.75, indicating that deviations of this magnitude might be expected thru chance in three out of four trials. The comparison of observed with theoretical distributions follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed............	102	36	29	13	180
Calculated...........	101	34	34	11	180
Difference...........	+1	+2	—5	+2	0

Progenies of seven other purple F_2 plants (group 3, table 8) consisted of the four color types Ia, IIa, V, and VIa. Four of these F_2 plants were self-pollinated and gave a total of 164 F_3 plants. Four, including one that was also selfed, were backcrossed to green and yielded a total of 209 F_3 plants. For the progenies from selfed F_2 plants P = 0.20, and for those from backcrossed plants P = 0.57. There is, therefore, one chance in five

in the one case and considerably more than an even chance in the other case that deviations of the kind noted may have been due to errors of random sampling. The comparisons follow:

Color types		Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Selfed	Observed	95	31	23	15	164
	Calculated	92	31	31	10	164
	Difference	+3	0	—8	+5	0
Backcrossed	Observed	54	58	44	53	209
	Calculated	52	52	52	52	208
	Difference	+2	+6	—8	+1	+1

Seven self-pollinated F_2 purple plants gave progenies consisting of the four color types Ia, IIIa, V, and VIb (group 4, table 8). Here $P=0.75$, indicating that there are three chances in four that such deviations as are shown are due to chance. The comparison follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	318	114	111	42	585
Calculated	329	110	110	37	586
Difference	—11	+4	+1	+5	—1

Five F_2 purple plants from self-pollination gave only two color types (Ia and IIa) in F_3 (group 5, table 8). The total number of F_3 individuals was 183, of which 139 were of color type Ia and 44 were of color type IIa, the expected numbers being, respectively, 137 and 46, and the deviation equaling 2 ± 4. One of these F_2 plants was also backcrossed to two greens, resulting in 12 purple and 9 sun red F_3 plants where equality of the two classes was expected. The deviation here is 1.5 ± 1.5.

Finally, two self-pollinated F_2 purple plants produced 217 F_3 individuals (group 6, table 8) of color types Ia and IIIa. There were 168 purple

and 49 dilute purple where the expected numbers were 163 and 54, respectively — a deviation of 5 ± 4.3.

It is seen, then, that in every case the F_3 progenies of F_2 purple plants were of color types expected on the basis of the three-factor hypothesis, and that the F_3 distributions within any group were in close agreement with expectation. It is particularly noteworthy, however, that not all types of F_3 behavior were observed, and that the distribution of the progenies of the thirty-five F_2 plants tested was in rather imperfect agreement with expectation. Thus, no F_2 purple plant bred true in F_3 where one such plant was expected, and none gave progenies of purple and brown only where at least two with such behavior were expected. It has already been pointed out (page 35) that eight classes of behavior of F_2 purples are looked for, and that any twenty-seven F_2 purple plants should be distributed with respect to their F_3 behavior in the relation 1:2:2:2:4:4:4:8. The actual and theoretical distributions are compared as follows:

Observed	0	5	2	0	5	7	7	9	35
Calculated	1.3	2.6	2.6	2.6	5.2	5.2	5.2	10.4	35.1
Difference	—1.3	+2.4	—0.6	—2.6	—0.2	+1.8	+1.8	—1.4	—0.1

While mere inspection of the above comparison might suggest poor agreement between theory and observation, nevertheless P = 0.36, indicating that such deviations as occur might be expected in more than one out of three trials, which is not a bad fit. So far, therefore, the available data are in fair accord with the three-factor hypothesis.

Before taking up a consideration of the F_3 behavior of other F_2 color types, it will be well to consider briefly the F_4 behavior of F_3 purple plants. Only one F_3 purple of the lot having all six color types (table 8, group 1), comparable to F_2 purples, was tested in F_4. This one plant gave an F_4 with the four color types Ia, IIa, V, and VIa.

Only eight other F_3 purple plants were tested in F_4. All these belonged to the lot consisting of color types Ia, IIIa, V, and VIb (group 4, table 8). The F_2 purple plants giving rise to this group are assumed to have been of the genotype *A a B b Pl Pl*. The F_3 purple plants should therefore have been of four genotypes and should have given F_4 behavior as follows:

F_3 genotypes	F_4 color types			
	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1 — *A A B B Pl Pl*.	1	....	....	....
2 — *A A B b Pl Pl*.	3	1	....	....
2 — *A a B B Pl Pl*.	3	....	1	....
4 — *A a B b Pl Pl*.	9	3	3	1

The data are presented in table 9. Four F_4 progenies (group 1) were made up of the four color types Ia, IIIa, V, and VIb. The total numbers of plants of each of the four types, as seen below, were in close accord with expectation, P equaling 0.57. There is more than an even chance that such deviations as those observed may have been due to errors of random sampling. The comparison of observed with calculated results follows:

Color types	Purple Ia	Dilute purple IIIa	Brown V	Green VIb	Total
Observed	185	68	74	20	347
Calculated	195	65	65	22	347
Difference	—10	+3	+9	—2	0

Three of the eight purple F_3's (group 2) gave in F_4 only purple and dilute purple plants, 88 of the former and 28 of the latter. The expected numbers were 87 and 29, respectively, showing a deviation of 1 ± 3.1.

One of the eight F_3 purples (group 3) gave 67 purple and 21 brown plants in F_4, while the expected numbers were 66 and 22, respectively. The deviation here is only 1 ± 2.7.

None of the eight F_3 purples bred true, but only one in nine was expected to do so. As already indicated, the theoretical distribution of nine F_3 purples of the sort here under consideration, with respect to the four kinds of behavior in F_4, is 1:2:2:4. The observed distribution was 0:3:1:4. There is more than an even chance that these deviations may have been due to errors of random sampling, P equaling 0.57.

It should not be forgotten that, while a very poor fit of observation to hypothesis, as measured by values of P, throws doubt upon the correctness of the hypothesis, it does not follow that a good fit proves the hypothesis to be true. This is particularly true where small numbers are dealt with. It will be recalled in this connection that, owing probably to the small numbers tested, no F_2 purple has been found to breed true in F_3 and none has been found to give only purple and brown offspring. It has been shown, however, that purple plants of the genotype *A a B B Pl Pl* exist, since one F_3 purple threw only purple and brown plants in F_4. Moreover, one of these F_4 purples repeated this behavior in F_5. Similarly it can be said that purples of the genotype *A A B B Pl Pl* have been recovered from the crosses under consideration, for two F_4 purple plants of the lot composed of purples and dilute purples (group 2, table 9), when backcrossed to green, gave 18 purple plants and no other types in the next generation, and one of these two F_4 purples, when crossed back to dilute sun red, gave 34 purple plants. Two other purples of the same F_4 lot, when similarly crossed, gave both purple and dilute purple, 23 of the former and 18 of the latter. Purple plants of all the expected genotypes have therefore been recovered in one or another generation from F_2 to F_4 from the original crosses of purple x green and dilute sun red x brown. Moreover, these genotypes have been found in numbers not far from what might reasonably be expected considering the relatively small numbers tested. It now remains to inquire into the F_3 and later behavior of F_2 color types other than purple.

Later behavior of F_2 sun red IIa.— Sun red plants of F_2 of the crosses purple x green and dilute sun red x brown are expected, in accordance with the three-factor hypothesis, to be of four sorts with respect to their behavior in F_3, as follows:

F_2 genotypes	F_3 color types		
	Sun red IIa	Dilute sun red IVa	Green VIa, c
1 — *A A B B pl pl*	1	....	....
2 — *A A B b pl pl*	3	1	....
2 — *A a B B pl pl*	3	....	1
4 — *A a B b pl pl*	9	3	4

Only nine F_2 sun red plants were tested by their F_3 behavior, and no later generations were grown. All the available data are given in table 10 (page 128). Five F_2 plants, when self-pollinated (group 1 of the table), gave the expected three classes of progeny, sun red, dilute sun red, and green, with a distribution of the F_3 plants as given below, and in addition a single brown plant. To include this unexpected plant in the comparison with the calculated distribution would give zero as the value of P, which is equivalent to saying that even in an infinite number of trials there is no chance of finding such a plant thru errors of random sampling. The single off-type plant is readily accounted for by supposing that a grain of foreign pollen was accidentally admitted in the pollination of the parent plant. Tho it is realized that, with such a convenient supposition always at hand, almost any result can be made to fit a theory, the reality of just such accidental pollinations will not be questioned by any one who has had experience in the technique of maize pollination. With the elimination of this one plant, the fit of observation to hypothesis is almost perfect. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	126	42	55	223
Calculated	125	42	56	223
Difference	+1	0	—1	0

Three F_2 sun red plants, including one of the five in the former test, were crossed back to green (group 1, table 10). The same three color types were observed as in the self-pollinated plants, with the addition again of a single off-type plant, this time a purple one. Even if this plant is left out of consideration as due to an accidental pollination, the fit of observed with calculated numbers is not very good. Such deviations from theoretical behavior are to be expected thru chance alone only once in eight trials, P equaling 0.12. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	14	18	50	82
Calculated	20.5	20.5	41	82
Difference	—6.5	—2.5	+9	0

A single F_2 sun red plant (group 2, table 10) gave, from self-pollination, 23 sun red and 9 dilute sun red F_3 plants, a deviation from expectation of 1 ± 1.7.

A single F_2 sun red plant (group 3, table 10), when crossed with green VIc, gave 50 sun reds and 43 greens where equality was expected, a deviation of 3.5 ± 3.3.

By way of summary of the behavior of F_2 sun red plants, it must be noted that, while four sorts of behavior were expected, only three sorts were observed. While any nine such F_2 plants should be distributed with respect to the four kinds of behavior in the relation 1:2:2:4, the observed relation was 0:1:1:7. While mathematically this is not a very bad fit considering the small numbers involved, P equaling 0.24, it is inadequate for a determination of the possible genotypes of F_2 sun red plants. Fortunately, certain crosses considered later (page 51) involving the sun red type, with presumably the same genetic constitutions as the F_2 sun reds of this cross, afford a more nearly adequate test of the matter.

Later behavior of F_2 dilute purple IIIa.— F_2 dilute purple plants should present the same types of behavior in F_3 as F_2 sun reds, but, of course, with somewhat different color types appearing, as follows:

F_2 genotypes	F_3 color types		
	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1 — *A A b b Pl Pl*	1	....	....
2 — *A A b b Pl pl*	3	1	....
2 — *A a b b Pl Pl*	3	....	1
4 — *A a b b Pl pl*	9	3	4

The available data from this test are given in table 11 (page 129). Four F_2 dilute purples (group 1) yielded the three color types expected, dilute purple, dilute sun red, and green, in the numbers shown below. There is considerably more than an even chance that the deviations from expectation may be due to errors of random sampling, P equaling 0.58. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	95	31	50	176
Calculated	99	33	44	176
Difference	—4	—2	+6	0

One of the dilute purple F_2 plants used in this test was backcrossed with green VIc (group 1, table 11), with the result shown below. There is practically an even chance that the observed deviations may be due to errors of random sampling, P equaling 0.49. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed	21	25	57	103
Calculated	26	26	52	104
Difference	—5	—1	+5	—1

One F_2 dilute purple gave 57 dilute purple and 21 dilute sun red plants in F_3 (group 2, table 11). The expected numbers were 58.5 and 19.5, respectively, the deviation being 1.5 ± 2.6.

Three F_2 dilute purples gave a total of 85 dilute purple and 20 green plants (group 3, table 11), the theoretical numbers being 79 and 26, respectively. The deviation from expectation, 6 plants, is just twice the probable error.

One F_2 dilute purple bred true in F_3, producing 21 dilute purple plants and no other types (group 4, table 11). Thus, all the sorts of behavior expected of F_2 dilute purples were realized in F_3. The distribution of the F_2 plants with respect to the four sorts of behavior was 1:1:3:4, instead of the theoretical distribution 1:2:2:4. Differences of this sort might be expected thru chance in four out of five trials, P equaling 0.80.

Only three plants of these lots were tested in F_4. One was a dilute sun red of the lot made up of dilute purples and dilute sun reds, and this one bred true in F_4 as was expected of it, producing 34 dilute sun red plants. The other two plants tested further were dilute purples of the lot containing the three color types III, IV, and VI. Both again gave these three

types, the total numbers of the respective classes being 29, 5, and 18. The expected numbers, 29, 10, and 13, show a deviation from expectation which might result thru chance about once in nine trials, P equaling 0.11.

Later behavior of F_2 dilute sun red IVa.— Dilute sun red plants of F_2 should be of two sorts, $A\,A\,b\,b\,pl\,pl$ and $A\,a\,b\,b\,pl\,pl$. Five such plants were tested, with results as shown in table 12 (page 129). Of these five, two bred true, producing a total of 92 dilute sun red plants (group 2). One of these two, when backcrossed with green, gave 69 dilute sun red plants. Three of the five F_2's gave in F_3 dilute sun reds and greens, 62 of the former and 17 of the latter (group 1). The theoretical numbers were 59 and 20, respectively. The deviation of 3 plants is only a little greater than the probable error, $\pm$ 2.6. With two of the F_2 dilute sun red plants breeding true and three again throwing segregates, expectation was very nearly realized.

Later behavior of F_2 brown V.— Brown plants of F_2 are expected to be of four genotypes and to show consequent differences in behavior in F_3 as follows:

F_2 genotypes	F_3 color types	
	Brown V	Green VI
1 — $a\,a\,B\,B\,Pl\,Pl$	1	......
2 — $a\,a\,B\,B\,Pl\,pl$	3	1
2 — $a\,a\,B\,b\,Pl\,Pl$	3	1
4 — $a\,a\,B\,b\,Pl\,pl$	9	7

Data for F_3 from fourteen F_2 brown plants are presented in table 13 (page 130). Five self-pollinated F_2 browns (group 1) gave, in addition to one sun red presumably due to accidental pollination, 96 browns and 74 greens in F_3, which is almost exactly a 9:7 relation, the deviation being 0.4 $\pm$ 4.4. Nine other selfed F_2 browns (group 2) gave in F_3 a total of 354 brown and 104 green plants. An exact 3:1 ratio for the total of 458 would be 343.5 and 114.5, respectively, the deviation being 10.5 $\pm$ 6.3. Such a deviation might be expected thru chance alone about once in four

trials. One of the F_2 brown plants that, when selfed, gave a 3:1 ratio in F_3, when crossed with green gave 34 brown and 41 green plants where equal numbers were expected, the deviation being 3.5 ± 2.9. None of the fourteen F_2 brown plants bred true in F_3. The fourteen plants should theoretically have given F_3 ratios of 1:0, 3:1, and 9:7 in approximately the respective numbers of 1.6, 6.2, 6.2, while the observed numbers were 0, 9, 5. Such deviations might occur by chance once in five trials, P equaling 0.22.

It is often difficult and sometimes practically impossible from ordinary F_3 progenies to distinguish between the two genotypes of brown which throw 3:1 progenies, namely, $a\,a\,B\,B\,Pl\,pl$ and $a\,a\,B\,b\,Pl\,Pl$. The green plants thrown by the former often show some brown pigment in the exposed parts of the sheaths and husks (type VIa), a condition not seen in the greens (VIb) thrown by the latter. In some lots the brown pigment is fairly conspicuous but in others it is very weak or is absent. Again, the greens of type VIb thrown by browns of the genotype $a\,a\,B\,b\,Pl\,Pl$ show considerable brown in the glumes of the staminate flowers. This is particularly pronounced when r^{ch} (a gene for cherry pericarp which is effective only in the presence of Pl) is present, but when this factor is lacking the brown color is often so faint that it is impossible to distinguish between a green plant carrying Pl and one lacking it. If r^{ch} is present, the green plants carrying Pl develop a light brownish pericarp at maturity while those lacking Pl never show this pericarp color whether or not B is present. Here again, however, the light brownish pericarp due to r^{ch}, Pl, and $a\,a$ may be wholly masked if there happens to be present another pericarp color gene, P, which with $a\,a$ brings about a strong brown color of the pericarp whether or not Pl or B is present.[4] On the whole, therefore, it is difficult, and often impossible, to determine the genotype to which a brown plant belongs, by an inspection of the green plants occurring in its progeny. Because of this, the 3:1 lots of F_3 progenies of F_2 brown plants are lumped together in group 2 of table 13 without any attempt to separate them into the two classes expected. Fortunately, it is readily possible to distinguish between brown plants of the two genotypes under consideration here by means of appropriate crosses.

[4] An account of these pericarp-color factors is to be published later by Dr. E. G. Anderson, who is making a study of the pericarp colors of maize.

When brown plants of all the genotypes expected in F_2 of the crosses of purple x green or dilute sun red x brown are crossed with homozygous dilute sun red plants, the following behavior is expected in the next generation:

F_2 genotypes	F_2 x *A A b b pl pl*			
	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1 — *a a B B Pl Pl*	1	....	....	....
2 — *a a B B Pl pl*	1	1	....	
2 — *a a B b Pl Pl*	1	....	1	....
4 — *a a B b Pl pl*	1	1	1	1

A few such tests of F_2 brown plants are recorded in table 14. Two plants (group 1), on being crossed with dilute sun reds, gave purples and sun reds only, 38 of the former to 45 of the latter, where equality was expected, the deviation being 3.5 ± 3.1. One of these plants has progeny from self-pollination listed in table 13, in group 2, the 3:1 lot. This plant was expected, of course, to throw only two color types from the cross with dilute sun reds, for otherwise it should not have given a 3:1 progeny on being selfed. The two brown plants in group 1 of table 14 must have been *a a B B Pl pl*. Two other F_2 brown plants (group 2) gave 32 purple and 38 dilute purple instead of the equal numbers expected, the deviation being 3.0 ± 2.8. These plants are assumed to have been *a a B b Pl Pl*. A single F_2 brown plant (group 3) when crossed with dilute sun red gave 15 purple plants, and is therefore assumed to have been *a a B B Pl Pl*.

The behavior of several F_3 brown plants when crossed with dilute sun reds is also shown in table 14. Three of these plants were from 9:7 F_3 lots and therefore are presumably comparable with F_2 browns. One of these three (group 4) gave the four color types I to IV in the numbers 1:2:6:3. It was probably *a a B b Pl pl* and should have given a 9:7 progeny if it had been selfed. The other two F_3 browns of the 9:7 lot gave 49 purple plants (group 7) and are consequently regarded as *a a B B Pl Pl*. All the other F_3 brown plants tested were from the

3:1 lot listed in table 13, group 2. None of these should give more than two types when crossed with dilute sun red. One gave 46 purple and 1 dilute sun red (group 7), the latter doubtless from an accidental pollination of the dilute sun red mother plant. Two F_3 browns gave 22 purple and 24 sun red plants (group 5), and four produced 73 purple and 85 dilute purple plants (group 6).

To summarize, all the theoretically possible genotypes of brown plants have been found either in F_2 or in such F_3 lots as showed a 9:7 ratio of brown to green. Since these F_3's are comparable with F_2 browns, they may be added to the F_2's in this summary. Of the twenty-one brown plants thus grouped, the numbers found to belong to each genotype are compared below with the calculated numbers. The deviations are such as might be expected to occur once in three trials, P equaling 0.34. The comparison follows:

	a a B B Pl Pl	*a a B B Pl pl* or *a a B b Pl Pl*	*a a B b Pl pl*	Total
Observed.......	3	12	6	21
Calculated......	2.3(+)	9.3(+)	9.3(+)	21
Difference......	+0.7(−)	+2.7(−)	−3.3(+)	0

Later behavior of F_2 green VI.— All F_2 green plants should breed true phenotypically in F_3. Data from eight such F_3 progenies are given in table 15, group 1 (page 132). There were observed a total of 179 green plants, and no other types. Progenies of sixteen green plants of the F_2 lots listed in tables 3 and 6 (pages 122 and 124), produced by backcrossing F_1 purples to greens, are given in table 15, groups 2 to 5. The total number of green plants in these progenies is 311. A single brown plant found in one of these progenies is assumed to have been due to accidental pollination. Green plants are therefore found to breed true green as expected, but there is nothing in this fact to indicate that green plants of the crosses under consideration are genotypically alike. That the five genotypes expected on the basis of the three-factor hypothesis were present among the progenies listed in table 15 is demonstrated in the next section of this paper.

Intercrosses of F_2 color types

It has been shown in the preceding pages that all the six color types occurring in F_2 of a cross between purple and green behave in F_3 and later generations as is expected on the basis of the three-factor hypothesis suggested to account for the F_2 results. It remains to determine whether the several color types behave in accordance with the hypothesis when intercrossed one with another. Of the fifteen possible intercrosses between phenotypically different types, two have already been discussed. The cross of purple with green has formed the basis of the whole discussion. The cross of dilute sun red with brown, since it was expected to give the same results as the original cross of purple with green, was most conveniently considered with that cross in generations later than F_2. The results of this second cross have been in accord with expectation. The other thirteen intercrosses are now to be considered, together with intercrosses of some types that are phenotypically alike.

Dilute sun red IVa x green VIa, VIb, VIc.—The progenies of self-pollinated green plants were listed in table 15 in several groups in accordance with what was learned of their genotypic constitution by the crosses to be considered here. The regular F_3 lots, from self-pollinated F_2 greens of self-pollinated F_1 purples, were put in group 1 of table 15. Only one of the same F_2 greens (table 16, group 2) was crossed with homozygous dilute sun red, *A A b b pl pl*. The result was 67 dilute purple plants. Another green plant, an F_3 from a self-pollinated F_2 green, gave, when similarly crossed, 9 dilute purple plants (group 2). Evidently both these green plants were *a a b b Pl Pl*. Four other F_3 green plants, when crossed with dilute sun red, gave a total of 148 sun red plants (group 1, table 16). One of these four belonged to an F_3 lot containing browns and greens in a 3:1 relation, and could not, theoretically, have done other than give all sun red or all dilute purple when crossed with dilute sun red. Two of the four were from greens of an F_3 lot made up of purples, sun reds, browns, and greens, and were therefore assumed to be *a a B B pl pl*, as the crosses with dilute sun red showed them to be. One of the four green plants, however, belonged to an F_3 lot of browns and greens in a 9:7 relation and was consequently comparable to an F_2 green. A sixth F_3 green also belonged to a 9:7 lot, comparable to an F_2 lot. When crossed with dilute sun red (group 3, table 16), it gave 24 dilute sun red plants,

and is therefore assumed to have been *a a b b pl pl*. All three of the theoretically possible homozygous genotypes have therefore been demonstrated among the F_2 greens or among F_3's comparable to F_2's.

In addition to the green plants of the direct F_2 and F_3 generations, noted above, fifteen other greens were crossed with dilute sun red. All these greens belonged to a single progeny, 2019, which was the result of a backcross of an F_1 purple with a green, *a a b b pl pl* (table 3, group 1). All of them should therefore have been heterozygous for *B* or *Pl*, or have lacked these dominant genes. Seven of the fifteen, when crossed with dilute sun red, gave 110 sun red and 85 dilute sun red plants (group 4, table 16), a deviation from equality of 12.5 ± 4.7. The green parent plants are consequently regarded as *a a B b pl pl*. Five others of the fifteen green plants (group 5) gave a total of 56 dilute purple and 65 dilute sun red, a deviation from equality of 4.5 ± 3.7, and hence are assumed to have been *a a b b Pl pl*. Three of the fifteen (group 6) gave a total of 106 dilute sun red plants. These three must, it is supposed, have been *a a b b pl pl*.

Naturally, in the course of the writer's maize studies, many other crosses between green and dilute sun red have been observed. But no purpose can be served by presenting here all this mass of data. Much of it has accumulated in connection with a study of the interrelations of plant and aleurone color, and will find its appropriate place in a later publication on that topic. A few F_2 and backcross progenies of dilute sun red F_1's of such crosses are, however, listed in table 17 (page 134), to serve as an indication of the behavior of all. Three F_2 progenies (group 1, table 17) contained 269 dilute sun reds and 99 greens, a deviation from the expected 3:1 ratio of 7 ± 5.6. Five progenies of F_1 dilute sun reds backcrossed to green VIc (group 2) included 357 dilute sun reds and 358 greens, a deviation from the expected 1:1 ratio of only 0.5 ± 9.0.

The behavior of a number of the sun red and dilute purple plants listed in table 16 has been studied in F_2 and later generations. Consideration of this later behavior is conveniently deferred to a later section of this paper (pages 51 and 53), where it is taken up with other crosses which should theoretically give similar results.

Green x green, VIa, VIb, VIc.— A number of green plants of progeny 2019, discussed above, were intercrossed. That these green plants bred true green when selfed was shown by the records of table 15 (groups 3

to 5). That they were of three distinct genotypes was shown by the data recorded in table 16 (groups 4 to 6). The behavior of random intercrosses of the same green plants is now to be considered. The data are given in table 18.

The green plants that served as parents of the crosses listed in group 6 of table 16, it was decided, must have been *a a b b pl pl*. When such plants are crossed with green plants of any of the other genotypes, nothing but green plants should result. A single cross of one of these greens with a green of the constitution *a a B b pl pl* (table 16, group 4) gave 23 green plants (table 18, group 1) as expected. Another cross of one of these greens with a green of the genotype *a a b b Pl pl* (table 16, group 5) gave 22 green plants (table 18, group 2). Crosses of green plants belonging to like genotypes should, of course, give only green plants. Three crosses of plants shown to be *a a B b pl pl* (table 16, group 4) gave 72 green plants (table 18, group 3). A single cross between plants shown to be *a a b b Pl pl* (table 16, group 5) gave 24 green plants (table 18, group 4). Five crosses of plants of genotype *a a B b pl pl* with plants of genotype *a a b b Pl pl* gave a total of 40 brown and 105 green plants (table 18, group 5). Here a 1:3 ratio of brown to green is to be expected. The theoretical numbers are therefore 36 and 109, respectively, and the deviation is 4.0 ± 3.5. The important fact here is that all these intercrosses of greens gave the color types expected on the basis of the results of crosses of the same individual green plants with dilute sun reds. The writer deems himself fortunate in having been able to obtain results approximating so closely a complete demonstration of the several genotypes of green, since the selfing, the crossing with dilute sun reds, and the intercrossing of greens, were made at the same time, with the green plants chosen wholly at random.

Brown V x green VIc.— When brown plants are crossed with green plants of type VIc, the F_1 plants are brown, and browns and greens alone appear in F_2. Since brown is supposed to be *a B Pl* and type VIc green *a b pl*, the F_2 progenies should exhibit 9:7 ratios. Eleven F_2 progenies are listed in table 19 (page 135), with a total of 317 brown and 223 green plants. The theoretical numbers are 304 and 236, respectively, showing a deviation of 13 ± 7.8. There is more than one chance in four that such a deviation is due to errors of random sampling, P equaling 0.27.

Of any nine F_2 brown plants of this cross, theoretically one should breed true in F_3, four should give a 3:1 ratio, and four should give a 9:7 ratio. Six F_2's were tested, with the results shown in table 20. Two bred true, with a total of 29 brown plants (group 1). Two gave ratios classed as 3:1, the totals (group 2) being 100 brown to 40 green, a deviation of 5.0 ± 3.5. Two gave progenies interpreted as 9:7 (group 3), totaling 39 brown and 39 green, the deviation being 5.0 ± 3.0. Of the 3:1 F_3 lot, two browns bred true in F_4, producing 59 brown plants, and one green bred true, producing 56 green plants.

The distribution of the F_2 brown plants with respect to their F_3 behavior — two breeding true, two throwing a 3:1 ratio, and two a 9:7 ratio — was as near expectation, 1:4:4 in nine, as could perhaps be expected from such small numbers. If these six F_2 browns are combined with the fourteen F_2 browns of the original cross of purple x green noted earlier in this paper (page 44), a very good fit of the hypothesis and observation is found ($\chi^2 = 0.88$). Theoretically these two lots of F_2 browns should be of the same genotypes, so that they may well be so combined. The comparison follows:

F_3 ratios	1:0	3:1	9:7	Total
Observed	2	11	7	20
Calculated	2	9	9	20
Difference	0	+2	—2	0

Sun red IIa x green VIc.— When both parents are homozygous, the cross of green of type VIc with sun red results in sun red plants only. Three such crosses gave 112 sun red plants. Crosses with heterozygous sun red plants gave F_1 progenies of sun red together with dilute sun red or green or both, depending presumably upon whether one or the other or both of the factors A and B were heterozygous. F_1 sun red plants of such crosses are presumed to have the formula $A\,a\,B\,b\,pl\,pl$, and should therefore produce in F_2 the three color types sun red, dilute sun red, and green, in the relation 9:3:4. Sixteen F_2 progenies of such crosses are listed in table 21, group 1 (page 136). It has already been shown (page 48) that crosses of some green plants, $a\,B\,pl$, with dilute sun reds, $A\,b\,pl$, give sun red F_1 offspring, which are also assumed to be $A\,a\,B\,b\,pl\,pl$. Five F_2 progenies of such crosses are, for convenience, considered here

(group 2, table 21) with the crosses of sun red and green. While certain of the individual progenies, due perhaps to the small numbers concerned, deviate considerably from the expected results, the twenty-one progenies (groups 1 and 2, table 21) taken together approach so closely to expectation that there is more than one chance in four that the observed deviations may be due to errors of random sampling, P equaling 0.28. The comparison of observed with expected numbers follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
IIa x VIc	827	268	383	1,478
IVa x VIa	343	120	179	642
Total	1,170	388	562	2,120
Calculated	1,193	398	530	2,121
Difference	—23	—10	+32	—1

F_1 sun red plants, *A a B b pl pl,* were also backcrossed with green plants of type VIc, *a b pl.* Fifteen progenies of these backcrosses are listed in table 21, the progenies from the cross IIa x VIc in group 3 and those from the cross IVa x VIa in group 4. The expected relation of 1:1:2 was realized fairly well in the results, the odds against the observed deviations' being due to chance being about three to two, P equaling 0.39. The observed and expected results are compared as follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed:				
(IIa x VIc) x VIc	134	123	267	524
(IVa x VIa) x VIc	442	465	962	1,869
Total	576	588	1,229	2,393
Calculated	598	598	1,196	2,392
Difference	—22	—10	+33	+1

Dilute purple IIIa x green VIc.— Since dilute purple differs from sun red merely in having the dominant *Pl* factor instead of *B*, crosses of dilute purple with green of type VIc should behave just as did the crosses considered in the preceding section, except that dilute purples take the place of sun reds in the progeny. Eight crosses of dilute purple with green of type VIc resulted in 91 dilute purple plants. The F_2 results of these crosses are given in table 22, group 1. Since the F_1 plants of these crosses are assumed to have been *A a b b Pl pl*, the F_2 results should be the same as those expected from crosses of greens of type VIb with dilute sun reds. The F_1's of the latter crosses have already been discussed (page 48). The F_2 results, six progenies, are for convenience considered here (group 2, table 22). While the expectation of a 9:3:4 relation was not very closely realized in the observed results, such deviations as those found might be expected thru chance about once in eight trials, P equaling 0.13. The comparison of observed and expected distributions follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c	Total
Observed:				
IIIa x VIc	416	149	173	738
IVa x VIb	274	102	107	483
Total	690	251	280	1,221
Calculated	687	229	305	1,221
Difference	+3	+22	—25	0

A single F_1 plant backcrossed with green gave the same three color types in the relation 26:20:56. The theoretical distribution is 25.5:25.5:51.0. Deviations of the observed order might be expected somewhat more than twice in five trials, P equaling 0.44.

Seven F_2 greens bred true in F_3 with a total of 359 individuals. One dilute sun red F_2 plant bred true with a progeny of 156 dilute sun red plants. Of the F_2 dilute purples, some bred true, some threw the three types seen in F_2, some gave only dilute purple and dilute sun red, and some gave only dilute purple and green. Notwithstanding the rather poor fit in F_2, therefore, the fact that practically all the expected classes

of behavior were exhibited in F_3 makes it seem likely that the deviations in F_2 were due mainly to chance.

Sun red IIa x brown V.— A single cross of brown with sun red gave purple plants only, as was expected. Since both parents were homozygous, all the F_1 plants should have been of the genotype *A a B B Pl pl* and should have produced in F_2 the four types purple, sun red, brown, and green, in the relation 9:3:3:1. The three F_2 progenies of this cross are recorded in table 23 (page 137). The expected color types were produced in approximately the expected numbers. The odds against the observed deviations' being due to chance are three to two, P equaling 0.40. A comparison of observed with expected distributions follows:

Color types	Purple Ia	Sun red IIa	Brown V	Green VIa	Total
Observed	120	29	37	10	196
Calculated	110	37	37	12	196
Difference	+10	—8	0	—2	0

Purple Ia x brown V.— Crosses of brown with purple gave purple F_1's, and four F_2 progenies gave a total of 116 purple and 38 brown plants, which is very near the 3:1 ratio expected from F_1 plants of the genotype *A a B B Pl Pl*, the deviation being 0.5 ± 3.6. Nine F_1 purples backcrossed to browns gave progenies totaling 484 purple and 477 brown plants, a deviation from the expected equality of 3.5 ± 10.5.

Purple Ia x sun red IIa.— Purples and sun reds should differ by a single factor pair, *Pl pl*. The F_1 purples backcrossed to sun red should give a 1:1 ratio of the parental types. Five such backcrosses gave 47 purple and 57 sun red plants, a deviation from expectation of 5 ± 3.4. No progenies of selfed F_1's were observed.

Purple Ia x dilute purple IIIa.— Purples are assumed to differ from dilute purples by the factor pair *B b*. Six F_1 purples backcrossed with dilute purple gave 40 purple and 52 dilute purple plants. This is a deviation from the expected equality of 6 ± 3.2. No other tests of the cross of purple x dilute purple were made.

Sun red IIa x dilute sun red IVa.— Sun reds and dilute sun reds should differ in one factor pair, *B b*, and should therefore give a simple 3:1 result in F_2. The F_1 generation of six crosses of these color types consisted of 135 sun red plants. Sixteen F_2 progenies listed in group 1 of table 24

(page 138) totaled 998 sun red and 314 dilute sun red, a deviation from the 3:1 ratio of 14 ± 10.6.

Fourteen backcrosses of F_1 sun red plants with dilute sun reds (group 2, table 24) resulted in 811 sun reds and 742 dilute sun reds, a deviation from the expected equality of 34.5 13±.3.

Two F_2 dilute sun reds bred true in F_3 as expected (table 25, group 1), with a total of 50 dilute sun red offspring. Two F_2 sun red plants (group 2) gave a total of 19 sun reds in F_3, and a third F_2 plant, on backcrossing with dilute sun red, gave 101 sun reds. Four other F_2 sun red plants gave both sun reds and dilute sun reds in their F_3 progenies (group 3), the respective numbers being 373 and 127; the calculated numbers are 375 and 125, respectively, showing a deviation of 2 ± 6.5. Of the seven F_2 sun reds tested, four were heterozygous and three apparently homozygous for the *B* factor. On the whole, therefore, the crosses of sun red with dilute sun red behaved approximately as expected.

Dilute purple IIIa x dilute sun red IVa.— Five crosses of dilute sun red with dilute purple gave a total of 344 F_1 plants, all dilute purple. Since these F_1's are supposed to be heterozygous for the *Pl* factor only, a 3:1 F_2 distribution of color types should result. Seven F_2 progenies listed in group 1 of table 26 (page 139) had a total of 261 dilute purple and 87 dilute sun red plants, exactly a 3:1 relation. Five F_1 plants were backcrossed with dilute sun red (group 2) and resulted in 275 dilute purples and 263 dilute sun reds. The deviation from the theoretical 1:1 relation is 6 ± 7.8.

Only two F_2 dilute purples were tested by their F_3 behavior. Neither bred true, the total produced being 38 dilute purples to 17 dilute sun reds, a deviation from the 3:1 ratio of 3.3 ± 2.2. As far as they go, then, the results are in close agreement with what is expected of the crosses here under consideration.

Sun red IIa x dilute purple IIIa.— Theoretically, crosses of sun red, *A B pl*, with dilute purple, *A b Pl*, should give purple, *A B Pl*, in F_1. Two crosses, as shown in group 1 of table 27 (page 140), gave a total of 24 purple and no other types. Here the parents were doubtless homozygous. If one or the other of the parents is heterozygous, two color types are to be expected in F_1. A single cross (group 2, table 27) gave 74 purple and 75 sun red plants. Such a result is to be expected when the sun red parent is homozygous, *A A B B pl pl*, and the dilute purple parent is heterozygous, *A A b b Pl pl*. Two other crosses (group 3) gave

a total of 28 purple and 29 dilute purple plants. The parents are therefore assumed to have been $A\ A\ B\ b\ pl\ pl$ and $A\ A\ b\ b\ Pl\ Pl$, tho the same results should have been obtained if one or the other, but not both, of the parents had been $A\ a$. The important point here is that purple plants were produced in all crosses, showing that sun red and dilute purple carry complementary factors for purple. The factors are assumed, in keeping with the hypothesis under test, to be B and Pl.

In accordance with this hypothesis, the F_1 purple plants should be $A\ A\ B\ b\ Pl\ pl$ and should throw four color types in F_2. No direct F_2 progenies have been observed, but seven progenies from backcrosses of F_1 purples with dilute sun reds are recorded in table 28. While the deviations from the expected equality among the four classes are rather large, they are not greater than might occur by chance about once in four trials, P equaling 0.26. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	99	110	104	83	396
Calculated	99	99	99	99	396
Difference	0	+11	+5	—16	0

Purple Ia x dilute sun red IVa.— Crosses of purple with dilute sun red should give purple F_1 plants, $A\ A\ B\ b\ Pl\ pl$, and 9:3:3:1 F_2 progenies. Four such crosses resulted in 65 purple plants in F_1. The F_2 results are reported in table 29, group 1. The distribution of the individuals of the twenty-six progenies taken together is shown below in comparison with the calculated distribution. The four color types expected were observed in approximately the expected numbers. Deviations such as shown might be expected thru chance about twice in eleven times, P equaling 0.18.

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	1,013	316	296	100	1,725
Calculated	970	323	323	108	1,724
Difference	+43	—7	—27	—8	+1

Some of the F_1 purple plants were crossed back to dilute sun red, with results as given in group 2 of table 29 and summarized below. The seventeen progenies together approached the expected equality of the four color types so closely that the observed deviations might be expected thru chance more than twice in five trials, P equaling 0.44.

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	323	306	325	289	1,243
Calculated	311	311	311	311	1,244
Difference	+12	—5	+14	—22	—1

Sixteen F_2 purple plants were tested by their F_3 progenies (table 30). Seven F_2 purples (group 1) gave again the four color types purple, sun red, dilute purple, and dilute sun red, the several classes being represented by 268, 105, 78, and 28 individuals, respectively, while the calculated numbers were 269, 90, 90, and 30. The odds against such deviations being due to chance are about three to one, P equaling 0.24. One of the seven F_2 purple plants was crossed with green *a a b b pl pl* and gave the same four classes of progeny, represented by 26, 25, 24, and 21 plants, respectively. Evidently these F_2 purples were like the F_1's, *A A B b Pl pl*.

Four other F_2 purples (group 2, table 30) gave only purple and sun red progenies. Three of these when selfed gave 60 purple and 22 sun red. Two of these three and one other, when backcrossed with dilute sun red or green, gave 32 purples and 31 sun reds. The four F_2's are therefore regarded as *A A B B Pl pl*.

Five F_2 purples (group 3) gave purples and dilute purples only. Four of these, which were selfed, gave 162 purples and 48 dilute purples, while the fifth, which was backcrossed to dilute sun red, gave 17 purples and 15 dilute purples. These five F_2's are consequently regarded as *A A B b Pl Pl*.

None of the sixteen F_2 purples tested bred true in F_3, *A A B B Pl Pl*. A single F_3 purple (group 6), however, which occurred in the F_3 lot showing the four color types (group 1) and which was therefore comparable to the F_2 purples, bred true in F_4, producing 69 purples on being selfed and 18 on being backcrossed to green. Of three other F_3 purples of the same

F_3 lot, two (group 4) gave only purples and sun reds, and one (group 5) gave only purples and dilute purples.

The twenty F_2 and F_3 purples tested, therefore, were distributed with respect to the four kinds of behavior in the relation 7:6:6:1, in contrast to the calculated distribution of approximately 8.9:4.4:4.4:2.2. There is more than an even chance that such a difference may be due to errors of random sampling, P equaling 0.53. On the whole, therefore, the F_2 purples of this cross behaved in later generations as was expected of them.

F_2 sun red plants of the cross purple x dilute sun red showed two types of behavior in F_3 (table 31, group 1). Three F_2's bred true, with 53 sun red plants in F_3. Four gave a total of 70 sun red and 24 dilute sun red plants. Where an expected ratio of one true breeding to two segregating progenies was expected, the observed relation of three to four is not a bad fit.

F_2 dilute purples also showed the two types of behavior expected in F_3 (group 2, table 31). Three bred true, with a total of 97 dilute purple plants, and six gave a total of 217 dilute purple and 86 dilute sun red plants. The 1:2 ratio was therefore exactly realized.

Three F_2 dilute sun reds bred true in F_3 (group 3) as was expected of them, producing a total of 72 dilute sun red plants.

Numerous F_3 plants of the several color types of the cross under consideration here were tested by F_4 and F_5 progenies, with results wholly consistent with expectation. It is deemed unnecessary to give the records of these later generations in detail.

Evidence from aleurone-color and linkage relations

The evidence presented up to this point in support of the three-factor hypothesis, involving *A a*, *B b*, *Pl pl*, has had to do with the behavior of the several F_2 color types in later generations and in intercrosses. There remain to be discussed some bits of evidence which, while less direct, are perhaps no less trustworthy. This evidence deals with (1) the relation of aleurone color to plant-color types, (2) the linkage of certain plant-color types with endosperm color, and (3) the linkage of other color types with the liguleless leaf.

Relation of aleurone color to plant color.— Of the plant-color factors considered in this section of the paper, the pair *A a* is concerned also in the development of aleurone color. It has been shown by the writer

in a previous paper (Emerson, 1918) that the presence of three dominant factors, A, C, and R, is necessary for the development of aleurone color. It is assumed that the factor pair $A\,a$ for aleurone color is identical with the pair $A\,a$ for plant color. Some of the evidence on which this assumption is based may well be considered at this point in order to justify the use of the same symbols for both plant and aleurone color. After the identity of $A\,a$ has been established, certain relations of aleurone color to plant color can be used to check up some of the conclusions previously drawn with respect to the genetic interrelations of the several plant-color types.

It will be recalled that dilute sun red crossed with green gave dilute sun red in F_1 and a 3:1 ratio of the two types in F_2 (table 17, group 1, page 134), and that backcrosses of F_1 with green gave a 1:1 ratio (group 2). The F_2 seeds of these F_1 plants also exhibited a 3:1 relation — 424 colored and 127 colorless, deviation 10.8 ± 6.9 — thus showing that only one factor pair, $A\,a$, $C\,c$, or $R\,r$, was heterozygous. The colorless seeds produced 98 green plants, and the colored ones produced 269 dilute sun reds and 1 weak plant, recorded as green, which died in the seedling stage. Obviously the factor that differentiates dilute sun red from green is the same as the one that in these cases differentiated the colored from the colorless seeds, or some factor very closely linked with it. Fortunately, F_1 plants closely related to the ones which when selfed showed the behavior noted above, were backcrossed with green, colorless-seeded A testers (Emerson, 1918). Of the resulting seeds 632 were colored and 590 were colorless, evidently a 1:1 relation — the deviation being 21 ± 11.8 — showing that the F_1 plants were, with respect to aleurone color, $A\,a\;C\,C\;R\,R$. The colored seeds gave rise to 357 dilute sun red plants and the colorless seeds to 358 green plants. Evidently, therefore, it is the $A\,a$ pair that differentiates dilute sun red from green. This is in support of the assumed genotypes $A\;b\;pl$ and $a\;b\;pl$ for dilute sun red and green, respectively.

The single progeny recorded in group 3 of table 9 (page 127) came from a plant known to be $A\,a$ with respect to aleurone color and producing 130 colored and 41 colorless seeds. The 3:1 aleurone-color relation shows it to have been heterozygous in only one aleurone-color factor, and therefore $A\,a\;C\,C\;R\,R$. The colored seeds, $A\;C\;R$, produced 67 purple plants, and the colorless ones, $a\;C\;R$, produced 21 brown plants.

Evidently, purples are differentiated from browns by the $A\,a$ pair alone, just as dilute sun reds are differentiated from greens. This is quite in keeping with the assumed genotypes, $A\,B\,Pl$ and $a\,B\,Pl$, for purple and brown, respectively.

Two of the progenies recorded in group 3 of table 8 (page 126) involved both aleurone and plant color. The heterozygous parents were back-crossed with green A testers and produced 125 colored and 127 colorless seeds. The factor pair differentiating these two seed classes was therefore $A\,a$. The colored seeds, $A\ C\ R$, produced 15 purple and 14 sun red plants, while the colorless seeds, $a\ C\ R$, gave 9 brown and 14 green plants. Since it is shown in the preceding paragraph that purples and browns differ with respect to the pair $A\,a$ alone, it may be inferred that the sun reds and the greens of these lots also differed with respect to $A\,a$ alone. The assumption heretofore made with respect to the genotypes of these color classes, $A\ B\ Pl$, $A\ B\ pl$, $a\,B\,Pl$, and $a\,B\,pl$, for purple, sun red, brown, and green, respectively, is given support by this relation of aleurone color to plant color.

Two of the progenies recorded in group 1 of table 9 (page 127), and one in group 4 of table 8 (page 126), were grown from self-pollinated plants known to be $A\,a$ with respect to aleurone color and found to have 644 colored and 228 colorless seeds. The 3:1 seed-color relation shows them to have been $A\,a\,C\,C\,R\,R$. The colored seeds, $A\ C\ R$, gave 294 purples and 113 dilute purples, while the colorless seeds, $a\ C\ R$, gave 119 browns and 40 greens. If purples and browns differ with respect to $A\,a$ alone, as they have been shown to do, presumably the dilute purples and the greens of these lots also differ in the same way. This is in keeping with the assumption that the genotypes of the color classes are $A\ B\ Pl$, $A\ b\ Pl$, $a\ B\ Pl$, and $a\,b\,Pl$, for purple, dilute purple, brown, and green, respectively.

These comparisons of the relations of aleurone color to plant color have confirmed definitely the supposition that purples, sun reds, dilute purples, and dilute sun reds have the dominant factor A, and browns and greens the recessive factor a. The comparisons have also afforded some support for the assumed genetic constitution of the several color types with regard to $B\,b$ and $Pl\,pl$. More definite evidence for the latter, however, is afforded by the linkage relations now to be discussed.

Linkage of plant color with endosperm color.— It has been known since 1912 that a linkage exists between the factor pair $Pl\,pl$ and endosperm

color. The data suggest irregularities or complexities which cannot be straightened out until more definite information is at hand with regard to the two or more factor pairs concerned in the development of yellow endosperm.[5] Only such data are presented here as are necessary to show the relations of the several plant-color types to endosperm color.

A single progeny recorded in table 27, group 2 (page 140), was made up of 74 purple and 75 sun red plants. The lot resulted from a cross of a white-seeded sun red plant with a dilute purple plant which was heterozygous with respect to both yellow endosperm and plant color. The yellow seeds produced 58 purple and 20 sun red plants, and the white seeds produced 16 purple and 55 sun red plants. The yellow-seeded sun reds and the white-seeded dilute purples are known to be the crossover classes. The ratio of non-crossovers to crossovers is 113:36, and the percentage of crossing-over, therefore, is 24.2. Evidently a factor pair for yellow endosperm, *Y y*, is linked with the factor pair that differentiates purple from sun red. In accordance with the hypothesis under test, this plant-color factor pair is *Pl pl* — purple = *A B Pl*, and sun red = *A B pl*.

Two other progenies (table 26, group 1, page 139) had a total of 116 dilute purple and 42 dilute sun red plants. The selfed parent plants were heterozygous for yellow endosperm as well as for plant color. The yellow seeds gave 99 dilute purple and 17 dilute sun red plants, and the white seeds gave 17 dilute purple and 25 dilute sun red plants. This F_2 distribution, as shown below, is very close to expectation ($\chi^2 = 0.26$) on the basis of 25 per cent of crossing-over between the factor pair *Yy* and the pair that differentiates dilute purple from dilute sun red. It seems likely, therefore, that the same plant-color factors, *Pl pl*, are concerned here as in the progeny consisting of purples and sun reds. This is in keeping with the theoretical genotypes, *A b Pl* and *A b pl*, assumed for dilute purple and dilute sun red, respectively. The comparison between the observed F_2 distribution and that calculated on the basis of 25 per cent of crossing-over follows:

Observed	99	17	17	25	=	158
Calculated	102	17	17	23	=	159
Difference	—3	0	0	+2		—1

[5] This problem is being investigated by Dr. E. G. Anderson.

A single progeny (table 8, group 3, page 126) from a selfed parent heterozygous for yellow endosperm, contained purple, sun red, brown, and green plants, totaling 63, in the relation 35:15:6:7. These four color types are expected to occur in a total of 64 in the relation 36:12:12:4 from a selfed plant of the genotype *A a B B Pl pl*. The observed deviation from expectation might occur by chance once in nine trials, P equaling 0.11. Theoretically, the green plants of this lot, *a B pl*, are differentiated from the browns, *a B Pl*, by the same factor pair, *Pl pl*, that differentiates the sun reds, *A B pl*, from the purples, *A B Pl*. If this is true, the same linkage relations should exist for yellow endosperm with the brown-green lot as with the purple-sun-red lot. From yellow seeds there came 29 purples and 8 sun reds, and from white seeds 6 purples and 7 sun reds. Such a distribution should be very closely realized ($\chi^2 = 0.97$) from 30 per cent crossing-over between *Y y* and *Pl pl*. The yellow seeds produced also 5 brown and 3 green plants, and the white seeds 1 brown and 4 green plants. While the number of individuals is too small to give a reliable indication, it is of interest to note that the coefficient of association (Collins, 1912) calculated from the series 5:3:1:4, or 0.739, is practically that calculated from 26 per cent of crossing-over. In so far as these records go, therefore, they support the assumption that brown and green in this lot are differentiated by the same factor pair as are purple and sun red, and thereby support the hypothesis under test.

A plant heterozygous for the three plant-color pairs *A a*, *B b*, *Pl pl*, and for *Yy*, backcrossed with a white-seeded green plant of type VIc, *a b pl y*, gave the six color types, purple, sun red, dilute purple, dilute sun red, brown, and green, in the numerical relation 10:13:17:11:9:33 (table 6, page 124), which is a close fit (P = 0.61) to the expected relation, 1:1:1:1:1:3. From yellow seeds the resulting series was 8:6:13:2:7:17, and from white seeds it was 2:7:4:9:2:16. When the classes having *A Pl*, purple and dilute purple, were lumped together, and similarly those having *A pl*, sun red and dilute sun red, the yellow seeds gave 21 plants with *Pl* and 8 with *pl*, while the white seeds gave 6 with *Pl* and 16 with *pl*. Of these 51 plants, there were 14 in the crossover classes, or a percentage of crossing-over of about 27.5 ± 4.1, approximately the same as in the cases cited above. In this lot there are theoretically three kinds of greens, *a B pl*, *a b Pl*, and *a b pl*, one of which has *Pl* and two of which have *pl*, while all the browns, *a B Pl*, have *Pl*. If there be

assumed 25 per cent of crossing-over between *Y y* and *Pl pl,* equivalent to a 3:1:1:3 gametic series, yellow seeds should give 3 brown to 5 green, and white seeds 1 brown to 7 green, as shown below:

	Yellow	White
Brown, *a B Pl*	3	1
Green, *a B pl*	1	3
Green, *a b Pl*	3	1
Green, *a b pl*	1	3
	5	7

The yellow seeds actually gave 7 brown to 17 green and the white seeds 2 brown to 16 green, which is a close fit to the calculated relation, 3:5: 1:7 (P = 0.59). In this case as in the others, then, the linkage relations between *Y y* and *Pl pl* afford additional support for the belief that the several color types actually bear to one another the relation assumed in the assignment of hypothetical genetic formulae (page 32).

Linkage of plant color with leaf type.— It has been known for some years that a leaf type termed *liguleless* (Emerson, 1912) is linked with the factor pair that differentiates sun red from dilute sun red. As an illustration of this, two backcross progenies, 8250 and 8253, with a total of 145 sun red and 147 dilute sun red plants, may be cited. These progenies came from a cross of normal-leaved sun red, *A B pl Lg,* with liguleless-leaved dilute sun red, *A b pl lg,* backcrossed with liguleless dilute sun red. Of the normal-leaved plants 104 were sun red and 41 were dilute sun red, while of the liguleless-leaved plants 48 were sun red and 99 were dilute sun red. The non-crossovers were to the crossovers as 203:89, or a percentage of crossing-over of 30.5. Since the factor pair that differentiates sun red from dilute sun red has been assigned the symbol *B b,* the linkage noted here is evidently between *B b* and *Lg lg.*

Six progenies from backcrosses of heterozygous normal-leaved purples with liguleless dilute sun reds gave purples, sun reds, dilute purples, and dilute sun reds in the relation 197:177:178:167, which is not far from the equality expected, P equaling 0.46. Among the normal-leaved plants, the four color types occurred in the relation 123:117:47:55, and among the liguleless-leaved plants in the relation 74:60:131:112. Evidently the purples bear the same relation to the dilute purples as the sun reds do to

the dilute sun reds. For sun reds and dilute sun reds, the non-crossovers are to the crossovers as 229:115, or a crossover percentage of 33.4 ± 1.7. For purples and dilute purples, the relation is 254:121, or a crossover percentage of 32.3 ± 1.5. It follows from this that the factor pair, *B b*, which differentiates sun red, *A B pl*, from dilute sun red, *A b pl*, is the same as that which differentiates purple from dilute purple. And this is in keeping with the hypothesis under test, in accordance with which purple and dilute purple have been assigned the genotypes *A B Pl* and *A b Pl*, respectively.

In a single progeny resulting from a backcross of a heterozygous normal-leaved purple plant with a liguleless-leaved green plant, greens occurred, as expected, with about three times the frequency of the average of the other five color classes. The progeny included 14 browns and 49 greens. Of the normal-leaved plants there were 10 browns and 19 greens, and of the liguleless-leaved plants 4 browns and 30 greens. On the basis of the hypothetical genotypes assigned to browns and greens, and with the assumption of 33 per cent of crossing-over between *B b* and *Lg lg*, the four classes, normal brown, normal green, liguleless brown, and liguleless green, should bear the relation 2:4:1:5. For a total of 63 plants, the relation would be approximately 11:21:5:26, whereas the observed relation was 10:19:4:30. The deviations from expectation are such as might occur by chance in more than three out of four trials, P equaling 0.78. In this case, as in the others reported, the linkage relations between *B b* and *Lg lg* afford support for the view that the several color types bear the relation to one another inferred from the hypothetical genotypes assigned them.

Summary of results involving A a, B b, Pl pl

The results of the cross of purple with green — which gave in F_2 six color types, namely, purple, sun red, dilute purple, dilute sun red, brown, and green, with a numerical relation of approximately 27:9:9:3:9:7 from selfed F_1's and about 1:1:1:1:1:3 from F_1's backcrossed to green — have been interpreted on the basis of the interaction of three factor pairs, *A a*, *B b*, and *Pl pl*. This hypothesis has been subjected to practically every genetic test available, as summarized below.

Each of the six F_2 color types has in turn been tested by its behavior in F_3, and in several cases behavior in F_4 and even in later generations

has been noted. All the possible combinations of intercrosses between the several types have been studied, except dilute purple x brown. In most cases these intercrosses have been carried to the F_2 generation, and in several instances to F_3 and F_4. Thruout the tests, the results have been in close agreement with those expected from the hypothesis. In almost every instance all the color types expected in each generation of the several crosses, and no others, have appeared. Moreover, the numerical relations found to exist between the several color types and also between the several classes of behavior have been reasonably close to expectation. It is true that in some instances the fit of observation to hypothesis has not been particularly good, but even here the observed deviations have been of such an order as might be expected to occur occasionally thru the chance errors of random sampling.

In addition to the tests afforded by the behavior of the several F_2 color types in later generations and in intercrosses, the relations of aleurone color involving the factor pair *A a* to the several plant colors, and the linkage relations of the plant-color factors *Pl pl* with the endosperm-color factors *Y y* and of the plant-color factors *B b* with the leaf-type factors *Lg lg*, have been included in the investigation. These tests have shown that the several color types bear to one another the relations to be deduced from the hypothetical genotypes assigned them.

The conclusion seems justified, therefore, that the three-factor hypothesis proposed as an interpretation of the F_2 results obtained in crosses of purple with green has been substantiated, in so far as it is possible to substantiate any hypothesis.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS B, B^w, b^s, b

In the preceding section of this account, six color phenotypes of maize have been discussed, namely, purple, sun red, dilute purple, dilute sun red, brown, and green. In addition to these six phenotypes, green plants have been shown to consist of three genotypes, which in some instances are slightly different phenotypically. Besides these six sharply separable phenotypes, there exist certain intermediate forms. The constancy of these types from year to year, under fairly uniform environmental conditions, leaves no doubt that they are genotypically as well as phenotypically distinct from the types considered heretofore.

One of these forms, known as weak purple, type Ib, is intermediate in certain respects between purple and sun red, and in other respects between purple and dilute purple. Plants of this type, prior to the flowering stage, frequently resemble sun reds more than purples. The pigmentation of the sheaths is less intense than with purples, and in some instances less than with strong sun reds. There is, however, sooner or later a tendency for pigment to develop on the stalk beneath the sheaths (Plate V, 2). In this respect weak purples resemble dilute purples as the latter often appear in a late stage of their development. The anthers of weak purples are usually full purple, like those of purples and dilute purples, in which respect they show no resemblance to sun reds.

A second intermediate form, known as weak sun red, type IIb, stands between sun red and dilute sun red. The sheaths and husks are less extensively and less intensely pigmented than is true of full sun red, and yet exhibit much more color than in dilute sun red (Plate V, 4). The anther color of weak sun red is like that of both sun red and dilute sun red.

While the difference between the extreme sun-color types, sun red and dilute sun red, is probably only a quantitative one — as is also presumably true of the difference between purple and dilute purple — little difficulty is experienced in separating sun red from dilute sun red plants on the one hand, or purple from dilute purple plants on the other. Frequently, however, it is difficult, or even impossible, at early stages of plant growth, to separate sun reds from purples. The existence of such intermediate forms as weak purple and weak sun red adds materially to the difficulties of classification. In fact, correct classification of all these types by inspection alone is possible only at the flowering stage. For certainty in classification, even at the flowering stage, environmental conditions, particularly soil fertility, must have been favorable thruout the growing period of the plants. While infertile soil exaggerates the difference between dilute sun red and green, by bringing about an excessive development of red pigment in the one type while no color develops in the other, on fertile soil only are revealed the finer distinctions between sun red, weak sun red, and dilute sun red. It is perhaps fortunate that the genetic relations of these several types are such that ordinarily not all of them occur in a single progeny.

Interrelations of sun red IIa, weak sun red IIb, and dilute sun red IVa

Numerous crosses of weak sun reds, IIb, with dilute sun reds, IVa, have given weak sun reds in F_1 and approximately three weak sun reds to one dilute sun red in F_2, just as crosses of strong sun red with dilute sun red give three strong to one dilute sun red (table 24, group 1, page 138). Records of such crosses are given in table 32 (page 144). Twelve F_2 progenies, totaling 1729 individuals, showed the two types in the relation 1300:429, almost exactly a 3:1 ratio, the deviation being 3.3 ± 12.1. The data for F_3 of these crosses are like those for crosses of strong sun red with dilute sun red (table 25). One weak sun red F_2 bred true in F_3 with a total of 77 weak sun red offspring (table 33, group 1). Four others gave both weak and dilute sun reds (group 2), in the relation 128:54, a deviation of 8.5 ± 3.9 from a 3:1 ratio. One dilute sun red bred true (group 3), with 95 dilute sun red plants in F_3.

A cross of weak sun red, IIb, with strong sun red, IIa, gave strong sun red in F_1 and the two parent types in F_2 in the relation 71:16, a deviation from the 3:1 ratio of 5.75 ± 2.72. There is, therefore, nearly one chance in six that the observed deviation may be due to errors of random sampling, P equaling 0.16.

In none of these crosses, strong with weak, weak with dilute, and strong with dilute sun red, have other than the parent types appeared in F_2. If weak sun red is due to the action of some additional modifying factor, not heretofore considered, types other than those of the parents should have occurred in some of the crosses. The natural conclusion, therefore, is that weak sun red, IIb, is due to an allelomorph of B and b, the pair concerned with the difference between sun red, IIa, and dilute sun red, IVa. This third allelomorph, responsible for weak sun red, may well be designated B^w.

Further evidence in support of the assumption that an allelomorph of B and b is concerned with weak sun red is afforded by linkage studies involving strong, weak, and dilute sun red with leaf type. Evidence has been offered (page 63) to show that $B\ b$ and $Lg\ lg$ are linked with about 30 to 33 per cent of crossing-over.

A single progeny, 8252, from a sun red plant heterozygous for leaf type and plant color backcrossed to liguleless weak sun red, contained 108 sun red and 109 weak sun red plants. Of the normal-leaved plants 80

were sun red and 38 were weak sun red, while of the liguleless-leaved plants 28 were sun red and 71 were weak sun red. The ratio of non-crossovers to crossovers is 151:66, or 30.4 ± 2.1 per cent of crossing-over. The percentage of crossing-over between *Lg lg* and the factor pair differentiating sun red and weak sun red, $B\ B^w$, is, therefore, practically the same as the linkage between *Lg lg* and *B b*.

Four backcross progenies, 8246–8249, involving sun red, contained 469 weak sun red and 396 dilute sun red plants. Of the normal-leaved plants 153 were weak sun red and 261 were dilute sun red, while of the liguleless-leaved plants 316 were weak sun red and 135 were dilute sun red. The non-crossovers are to the crossovers as 577:288, or 33.3 ± 1.1 per cent of crossing-over. Here again, therefore, the linkage between *Lg lg* and the factor pair differentiating weak sun red from dilute sun red, $B^w\ b$, is practically the same as that between *Lg lg* and *B b* or between *Lg lg* and $B\ B^w$.

From the facts (1) that in crosses between any two of the three types sun red, weak sun red, and dilute sun red, the third type is not produced, and (2) that the linkage value between *Lg lg* and the factor pairs differentiating weak sun red from sun red and from dilute sun red is approximately the same as that between *Lg lg* and *B b*, it seems evident that weak sun red is due to a factor B^w belonging to the triple allelomorphic series B, B^w, b.

It seems probable that this series of allelomorphs contains other members in addition to the three listed above, but there is at present little conclusive evidence in support of the idea. There are certainly several forms, commonly classed as dilute sun red, that differ considerably in the amount of red pigment developed, and certainly some of these differences are genetic. As is shown in the next section of this account, some of these differences, particularly with respect to silk, anther, and leaf-blade color, are due to the effect of the aleurone-color factors *R r*. Environmental conditions, particularly soil fertility, influence the development of this pigment so greatly that the problem becomes a difficult one. There is, however, some evidence that at least two forms of dilute sun red are differentiated by a factor pair belonging to the series B, B^w, b. These forms differ principally in the amount of color in the fresh husks (Plate VI, 1 and 2), and to some extent in the sheaths, which are the plant parts most strikingly different in sun red, weak sun red, and dilute sun red.

A type of dilute sun red with stronger husk pigmentation than ordinary dilute sun red shows was crossed with an ordinary dilute purple. Leaf type also was involved in the cross. The F_1 plants were dilute purples with somewhat more pigment in the husks of young ears than is usual with that type. A single progeny, grown from an F_1 backcrossed with liguleless dilute sun red of a light type, consisted of 25 dilute purples and 18 dilute sun reds. Each of these classes was sorted with some difficulty into light and more strongly colored subclasses, in accordance with the amount of color on the husks of the young ears. Of the more strongly pigmented dilute sun reds 4 had normal and 6 had liguleless leaves, while of the lighter dilute sun reds 6 had normal and 2 had liguleless leaves. Of the more strongly colored dilute purples 4 had normal and 13 had liguleless leaves, while of the lighter ones 4 had normal and 4 had liguleless leaves. While these numbers are small and the behavior was somewhat irregular, it is perhaps noteworthy that the factor pair differentiating the lighter from the more strongly colored plants, of both the dilute sun red and the dilute purple classes, exhibited an apparent linkage with $Lg\ lg$ of a value not far from that observed between $Lg\ lg$ and $B\ b$, $B\ B^w$, and $B^w\ b$. The observed percentages of crossing-over were 32.0 for the dilute purples, 33.3 for the dilute sun reds, and 32.6 for the entire lot. This evidence, slight as it is, plainly suggests a fourth member, b^s, of the B series of allelomorphs, which may be stated tentatively as B, B^w, b^s, b.

Relation of weak purple Ib to purple Ia, dilute purple IIIa, and weak sun red IIb

By methods similar in the main to those outlined above, Dr. E. G. Anderson has been able to show that weak purple is differentiated from purple on the one hand and from dilute purple on the other by the same factor, B^w, that differentiates weak sun red from sun red and from dilute sun red. At the time when Dr. Anderson undertook to determine the genetic relations of weak purple, nothing was known of the relation of weak sun red to sun red and dilute sun red as presented above. Furthermore, there was no indication as to whether weak purple was differentiated from purple and dilute purple by an allelomorph of $B\ b$ or of $Pl\ pl$, or by some distinct factor pair that might modify the ordinary result of the interaction of the pairs $A\ a$, $B\ b$, and $Pl\ pl$ then known to be concerned in the production of plant colors. The evidence to be presented here

is taken almost wholly from Dr. Anderson's records, and the conclusions derived from it are his. It is with Dr. Anderson's permission and at his suggestion that, for the sake of completeness of this account of the inheritance of plant colors, his results are here presented.

A cross of a weak purple Ib with a homozygous dilute purple IIIa resulted in 25 weak purples only, while a cross of another weak purple with a homozygous dilute purple, a sib of the plant used in the first cross, gave 63 weak purples and 53 dilute purples. Two of the F_1 weak purples were backcrossed to dilute purples, and a third to dilute sun red. The result (table 34, group 1, page 145) was 141 weak purples and 163 dilute purples, a deviation of 11 ± 5.9 from equality. Five crosses of weak purples with dilute sun reds gave a total of 32 weak purples and 25 dilute purples, a deviation from equality of 3.5 ± 2.5, while two other such crosses gave 29 weak purples only. Evidently these weak purple plants differed from dilute purples by a single factor pair. This pair could not have been *Pl pl*, for the crosses of weak purple with dilute purple, *A b Pl*, gave the same results as those with dilute sun red, *A b pl*. This leaves the possibility that *B b* or some unknown factor pair was concerned.

Three crosses of weak purple Ib with purple Ia resulted in 52 purple plants. A single cross of weak purple with sun red IIa gave 18 purples. Evidently both purple and sun red carry some factor that acts to change weak purple to purple. Unfortunately, no later generations of any of these crosses were grown, but it is evident from the F_1 results and from what is known of the interrelations of purple, sun red, and dilute purple that the dominant factor *B*, common to both purple and sun red, is concerned in the change from weak purple to purple. Since the crosses of weak purple with dilute purple, *A b Pl*, and with dilute sun red, *A b pl*, gave no purples, while crosses of weak purple with purple, *A B Pl*, and with sun red, *A B pl*, gave purple, the *Pl pl* pair is not concerned in the difference between weak purple and purple any more than in that between weak purple and dilute purple. These results, however, do not exclude the possibility that weak purple may be *A b Pl*, like dilute purple, with the addition of some unknown dominant modifying factor.

A single weak purple plant, which was, so far as known, unrelated to the weak purples considered above, when crossed with two unrelated dilute sun reds gave progenies consisting of 15 weak purples and 13 weak sun reds. Seven progenies of these F_1 weak purple plants backcrossed

with dilute sun reds are listed in table 34, group 2. These progenies consisted of four color types, weak purple, weak sun red, dilute purple, and dilute sun red, in the numerical relations given below:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	481	526	460	537	2,004
Calculated	501	501	501	501	2,004
Difference	—20	+25	—41	+36	0

The deviations from equality of the four classes expected of a dihybrid are so great that they would not occur by chance alone more than once in twenty trials, P equaling 0.05. Dr. Anderson's notes indicate that there was considerable difficulty, in the case of two of the cultures, in distinguishing dilute purple from dilute sun red. Whether this difficulty may account in part for the poor fit is not known. The outstanding fact, however, is the appearance of the four classes and no others. Since weak sun red is known to differ from dilute sun red by the factor pair B^w b, the inference is clear that weak purple differs from dilute purple by the same pair and by no others. The formulae assumed for the four color types are, therefore, $A\ B^w\ Pl$, $A\ B^w\ pl$, $A\ b\ Pl$, and $A\ b\ pl$, respectively.

If the foregoing conclusion is correct, crosses of weak sun reds with dilute purples should give weak purples in F_1 and the same four color classes in F_2 as are noted above for crosses of weak purple with dilute sun red. A single cross of a dilute purple with a homozygous weak sun red resulted in 16 weak purple plants. Two crosses of dilute purples with weak sun reds heterozygous for B^w b gave 12 weak purples and 11 dilute purples. That the production of weak purples in these crosses was not due to the b or Pl factors of the dilute purple parents is evidenced by the fact that crosses of the same dilute purple individuals with sun reds gave full purples in F_1. One of the F_1 weak purples, $A\ A\ B^w b\ Pl\ pl$, of the above crosses was backcrossed with dilute sun red, $A\ b\ pl$, with the result (table 34, group 3) shown below. The expected equality of the

four color types was closely approached in the results, χ^2 equaling 0.80. The comparison of observed with expected results follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	21	28	22	27	98
Calculated	24.5	24.5	24.5	24.5	98
Difference	—3.5	+3.5	—2.5	+2.5	0

The progeny of a purple plant heterozygous for $B\,B^w$, *Pl pl*, and the endosperm color pair *Y y*, backcrossed with a white-seeded weak sun red plant, $A\,B^w\,pl\,y$, affords evidence of another kind with respect to the interrelations of strong and weak purple and of strong and weak sun red. It has been noted previously (page 60) that *Pl pl* and *Yy* are linked, with a somewhat irregular percentage of crossing-over. The backcross gave the four color types purple, weak purple, sun red, and weak sun red, in the numerical relation 60:48:59:62. The observed deviations from the equality expected of a dihybrid are such as might occur by chance more than once in two trials, P equaling 0.54. The distribution of these 229 plants to the four color types when the progeny of yellow seeds and that of white seeds are considered separately is as follows:

Color types	Purple Ia	Weak purple Ib	Sun red IIa	Weak sun red IIb	Total
Yellow seeds	48	36	8	17	109
White seeds	12	12	51	45	120

Evidently weak purple, assumed to be $A\,B^w\,Pl$, here bears the same relation to weak sun red, $A\,B^w\,pl$, that purple, *A B Pl*, is known to bear to sun red, *A B pl*. In case of the purples and the sun reds alone, the linkage of *Pl pl* with *Y y* is shown by 99 non-crossovers to 20 crossovers, or 16.8 ± 2.7 per cent of crossing-over. When the weak purples and the weak sun reds are alone considered, the non-crossovers are to the crossovers as 81:29, a crossover percentage of 26.4 ± 2.8. While the

difference between these two percentages of crossing-over, 9.6 ± 3.9, is considerable, it is probably not statistically significant, P equaling 0.09.

Still further evidence in favor of the assumption that weak purple is differentiated from dilute purple by the factor pair B^w b, just as weak sun red is differentiated from dilute sun red, is afforded by data from six of the progenies recorded in group 2 of table 34. These data, it will be recalled, were obtained from F_1's of weak purple x dilute sun red backcrossed to dilute sun red. The F_1 weak purples were heterozygous for liguleless leaf as well as for plant color, $A\ A\ B^w\ b\ Pl\ pl\ Lg\ lg$, and the dilute sun reds with which they were backcrossed were liguleless, $A\ b\ pl\ lg$. The 1724 plants were distributed as follows:

Color types	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa	Total
Normal leaves............	296	315	119	164	894
Liguleless leaves..........	108	125	280	317	830

Evidently the linkage relations of liguleless with weak purple and dilute purple are similar to those already known for liguleless with weak sun red and dilute sun red (page 67). Of the 921 weak sun reds, $A\ B^w\ pl$, and dilute sun reds, $A\ b\ pl$, 632 belong to the non-crossover and 289 to the crossover class, a percentage of crossing-over of 31.4 ± 1.0. Similarly, of the 803 weak purples and dilute purples, the non-crossovers are to the crossovers as 576:227, a percentage of crossing-over of 28.3 ± 1.1. The difference between these two percentages of crossing-over, 3.1 ± 1.5, is such as might occur by chance once in six trials, P equaling 0.16.

By way of summary, it may be noted that, from appropriate intercrosses of the several color types and from determinations of the linkage relations of these types with liguleless leaf and with yellow endosperm, weak purple and weak sun red have been shown to have the genotypes $A\ B^w\ Pl$ and $A\ B^w\ pl$, respectively. This establishes the existence of the triple allelomorphs, B, B^w, b. There is some evidence in favor of the occurrence of a fourth member of this series, b^s.

CROSSES INVOLVING THE MULTIPLE ALLELOMORPHS R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

In an earlier section of this account (page 29) dealing with crosses involving only $A\ a$, $B\ b$, and $Pl\ pl$, three types of green plants were reported,

namely, $a\ B\ pl$ (VIa), $a\ b\ Pl$ (VIb), $a\ b\ pl$ (VIc). Still another type of green — a type wholly devoid of purple, red, or brown pigment — has been used in several crosses, with results quite unlike those obtained from corresponding crosses with the other green types. For reasons that become apparent later, this fourth type of green is regarded as genetically similar to dilute sun red and is known as type IVg.

Green IVg x brown V

Generations F_1 and F_2.— When brown, $a\ B\ Pl$, is crossed with green of any of the three types previously studied, brown appears in F_1 and brown and green in F_2. If green VIc, $a\ b\ pl$, is used in the cross, the F_2 ratio approaches 9:7, while if green VIa, $a\ B\ pl$, or VIb, $a\ b\ Pl$, is used, 3:1 F_2 ratios are of course expected (tables 19 and 20, page 135). In striking contrast with such results are those obtained from a cross of brown with green IVg. Two such crosses gave 78 purple plants in F_1, and a third cross resulted in 72 purple and 63 sun red plants. It will be recalled that just such results as these were obtained from crosses of dilute sun red with brown (tables 4 and 14, pages 123 and 131). The brown plant, 2031–20, which gave purple and sun red F_1 plants when crossed with green IVg, was the identical plant previously reported (table 4, group 2) to have given 55 purples and 55 sun reds when crossed with a dilute sun red plant. Moreover, this same brown plant was shown (table 20, group 2, page 135) to have produced from self-pollination 82 browns and 34 greens. Evidently it was $a\ a\ B\ B\ Pl\ pl$. The important point here is that crosses of brown with green IVg give exactly the same results in F_1 as if green IVg were a dilute sun red, $A\ A\ b\ b\ pl\ pl$.

There are other reasons, in addition to the F_1 results of crosses with brown, for supposing that green IVg has the factor A. When the pericarp-color gene P occurs together with A, the resulting pericarp color is always red, but when P and $a\ a$ are associated the pericarp color is brown. When green IVg plants have pericarp color it is red rather than brown, while that of greens VIa, VIb, and VIc is always brown. Again, the A factor is known to be essential to the production of aleurone color (Emerson, 1918), and the stock of IVg green plants used in these crosses, a strain of the variety Black Mexican sweet corn, was homozygous for purple aleurone. It is noteworthy in this connection that many, perhaps most, plants of this variety show very slight traces of sun red, and these traces are

limited commonly to the glumes of the staminate inflorescence. Apparently the stock of green IVg, which under no environmental conditions to which it has been subjected has ever been observed to produce the slightest trace of sun red, is merely an extreme minus variation of dilute sun red.

Not only were the F_1 results of the cross of brown with green IVg like those of the cross of brown with dilute sun red, but the same major color types appeared in F_2 (table 35, page 145). The distribution of all the individuals of six F_2 progenies to the six major color types heretofore recognized is compared below with the theoretical distribution calculated on the assumption that the green IVg parent was genotypically a dilute sun red, *A A b b pl pl*:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Observed........	309	100	67	19	88	98	681
Calculated.......	287	96	96	32	96	74	681
Difference.......	+22	+4	—29	—13	—8	+24	0

The outstanding features of this comparison are the relatively small deviations, in comparison with the number of individuals, for the purple, sun red, and brown types, and the relatively large deviations for the dilute purple, dilute sun red, and green classes. The relative importance of the several deviations is best seen by a comparison of the quotients of calculated frequencies into the squares of corresponding deviations, from which χ^2 and P are derived (Elderton's and Pearson's tables). These quotients for the several classes are:

Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green
1.69	0.17	8.76	5.28	0.67	7.78

If these quotients were no greater in the case of dilute purple, dilute sun red, and green than for purple, sun red, and brown, there would be about two chances in five that the observed deviations might be due merely to errors of random sampling, a fairly good fit being shown — $\chi^2 = 5.06$, $P = 0.41$. But as they stand, these deviations could be expected to occur thru chance alone not more than once in five thousand similar trials, a

very poor fit being shown — $\chi^2 = 24.35$, $P = 0.0002$. Evidently, green IVg does not give the same results in F_2 of this cross as does dilute sun red.

It is to be supposed, of course, that green IVg differs in some essential genetic way from dilute sun red, else it would not remain true green for generation after generation while the typical dilute sun red constantly produces a conspicuous amount of sun red pigment. It was therefore to be expected that the dilute sun red class would be deficient in F_2 while the green class would show a corresponding excess. But if the 24 green plants in excess of the calculated number be added to the dilute sun red class, that class becomes too large by eleven individuals, the excess now becoming almost as great as the observed deficiency. Moreover, the dilute purple class, it must be remembered, remains greatly deficient. If it be supposed that the excess of greens came about at the expense of dilute purples as well as of dilute sun reds, a very good fit of observation to theory is obtained. On redistribution of the 24 greens in excess of expectation to the dilute purples and dilute sun reds in the 3:1 relation usually existing between these classes, the corrected distribution for the six classes is as shown below. There are almost two chances in five that the deviations may be due to random sampling, P equaling 0.38.

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Corrected distribution	309	100	85	25	88	74	681
Calculated	287	96	96	32	96	74	681
Difference	+22	+4	—11	—7	—8	0	0

Mere closeness of fit cannot, of course, be regarded as proof of the supposition on which the corrected distribution was made. But there are other considerations which greatly strengthen the hypothesis. In the case of all the F_2 progenies listed in table 35, it was observed that some of the purple plants, altho quite as strongly colored otherwise as normal purples, had wholly green anthers in place of the usual dark purple ones (Plate I, 4). Likewise some of the sun red plants had green instead of pink anthers. In striking contrast to this, not a single dilute purple or dilute sun red plant with green anthers was seen in the whole lot, the dilute

purples, so far as observed, having dark purple anthers and the dilute sun reds pink anthers, just as in the lots considered in the first section of this paper. Counts of the purple and the sun red plants with different anther colors were made for only three of the six F_2 progenies (table 36), and for these lots not every plant was noted at the time when it was possible to determine the anther color positively. When some anthers have become dry and weathered, it is impossible to tell whether they were pink or green when fresh. Less difficulty is experienced with purple anthers, which hold their color much longer. Unfortunately, the records of the three F_2 families were not made early enough for positive identification of anther color of all plants. Of 162 purple plants, 117 had purple anthers and 33 had green anthers, while 12 were not recorded. Of 50 sun red plants, 21 had pink anthers and 12 had green anthers, with 17 not recorded. In these two lots the plants with purple and pink anthers were together about three times as numerous as those with green anthers, thus suggesting a simple monohybrid relation between colored and green anthers.

Working hypothesis.— If the genetic factor which is responsible for green anthers of purple and sun red plants be assumed to cause, in the case of dilute purples and dilute sun reds, not merely the anthers but the whole plant — leaves, sheaths, husks, glumes, stalk, and so forth — to be green, a satisfactory working hypothesis is afforded. The factor concerned here has been found to be the well-known aleurone-color factor *R*, or else some factor very closely linked with it. Some of the evidence on which this statement is based is presented later in this paper (pages 80, 98). It may be pointed out in passing that the relation between anther color and aleurone color here noted was studied by Webber (1906) some years before the several aleurone-color and plant-color factors had been determined.

Since aleurone color is not primarily concerned in the present account, it might be less confusing if the case were regarded as one of complete linkage, and if some other symbol for anther color were used and all reference to the *R* factor omitted in this paper. Until recently there was nothing known of aleurone-color behavior that made necessary the assumption of more than the simple factor pair, *R r*. The plant-color behavior, on the other hand, as becomes apparent later, necessitates the assumption of a group of multiple allelomorphs responsible in turn for diverse combinations of colors of leaves, sheaths, anthers, silks, and other plant parts. The commonest combinations in the writer's cultures are

strong pink anthers with deep red silks, lighter pink anthers with reddish or pinkish silks, green anthers with green silks, and so on, but there exist also such combinations as strong pink anthers with green silks, green anthers with reddish silks, and the like. Moreover, different intensities of dilute sun red in leaf blades, glumes, and other parts are sometimes combined with various silk-color and anther-color combinations. There is evidence that at least several of these combinations behave as would be expected if each were a definite unit allelomorphic to any one of the others.

Perhaps the most remarkable feature of this series of allelomorphs — or supposed allelomorphs — is the fact that a single unit behaves as a dominant with respect to the color of one plant part and as a recessive with respect to that of another part. Thus, a combination of dominant pink anthers with recessive green silks is common in the writer's cultures. The wholly green plants used in the crosses here under consideration are recessive for green silks, anthers, glumes, sheaths, husks, and other parts, and dominant for colored aleurone. Since the aleurone-color symbols $R\,r$ have long been employed in the usual way, R as the dominant and r as the recessive allelomorph, this usage is adhered to in this paper. The effect of these factors on plant color is indicated by superscripts. Thus, both R^r and r^r are dominant allelomorphs with respect to pink anthers and reddish silks, while both R^g and r^g are recessive for green anthers, silks, and so on. In the crosses here considered it is known that r^r and R^g are the pair concerned. With respect to plant color, therefore, as contrasted with aleurone color, r^r is dominant and R^g is recessive. While it is realized that this usage may tend to confuse the hasty reader, the use of any other symbols that have so far suggested themselves would result in greater confusion ultimately, particularly when the interrelations of plant color and aleurone color are taken up.

To return to the F_2 behavior of crosses of green IVg with brown, the following notation should express the F_2 results obtained, provided the proposed hypothesis is tenable:

Phenotypes	Plant color	Anther color
81 — $A\,B\,Pl\,r^r$ — *Ia*	Purple	Purple
27 — $A\,B\,Pl\,R^g$ — *Ig*	Purple	Green
27 — $A\,B\,pl\,r^r$ — *IIa*	Sun red	Pink
9 — $A\,B\,pl\,R^g$ — *IIg*	Sun red	Green
27 — $A\,b\,Pl\,r^r$ — *IIIa*	Dilute purple	Purple

Phenotypes	Plant color	Anther color
9 — $A\,b\,Pl\,R^g$ — *IIIg*	Green	Green
9 — $A\,b\,pl\,r^r$ — *IVa*	Dilute sun red	Pink
3 — $A\,b\,pl\,R^g$ — *IVg*	Green	Green
27 — $a\,B\,Pl\,r^r$ — *V*	Brown	Green
9 — $a\,B\,Pl\,R^g$ — *V*	Brown	Green
9 — $a\,B\,pl\,r^r$ — *VIa*	Green	Green
3 — $a\,B\,pl\,R^g$ — *VIa*	Green	Green
9 — $a\,b\,Pl\,r^r$ — *VIb*	Green	Green
3 — $a\,b\,Pl\,R^g$ — *VIb*	Green	Green
3 — $a\,b\,pl\,r^r$ — *VIc*	Green	Green
1 — $a\,b\,pl\,R^g$ — *VIc*	Green	Green
256		

The theoretical numerical relation between the several color combinations, in the order given above except that all greens are included in the last class, is 81:27:27:9:27:9:36:40, total 256.

The distribution of the 353 individuals of the three F_2 progenies for which anther records were made (table 36, page 146) is compared below with the theoretical distribution. In order that all plants may be included, the few purple and sun red plants whose anther colors were not noted are arbitrarily distributed to the colored-anther and green-anther classes in a 3:1 ratio. The fit of observation to hypothesis is so good that there are three chances in five that the deviations may be due to errors of random sampling, P equaling 0.60.

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Observed......	126	36	34	16	39	10	42	50	353
Calculated.....	112	37	37	12	37	12	50	55	352
Difference.....	+14	—1	—3	+4	+2	—2	—8	—5	+1

When the six F_2 progenies listed in table 35, for three of which no records of anther color were made, are grouped without reference to anther color, the comparison of observed and calculated numbers are as given below. For the six progenies there is practically an even chance that the deviations may be due to errors of random sampling, P equaling 0.48. It will be recalled that when these same progenies were compared with the dis-

tribution calculated on the basis of the three-factor hypothesis, the fit was very poor, P equaling 0.0002 (page 76). Comparison of the observed distribution with the distribution calculated on the four-factor basis follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	IIIg, IVg, VI	
Observed	309	100	67	19	88	98	681
Calculated	287	96	72	24	96	106	681
Difference	+22	+4	−5	−5	−8	−8	0

Relation of aleurone color to plant color.— It is evident from the comparisons already given that the four-factor hypothesis fits well the F_2 data, which is of course to be expected since it was invented for that purpose. But this fact alone is far from a substantiation of the hypothesis. The genetic tests ordinarily available are the behavior of the several F_2 types in later generations and in intercrosses. Since aleurone color as well as plant color is involved in these crosses, still another test can be employed. The six F_1 plants whose F_2 progenies are recorded in table 35 produced from self-pollination a total of 955 seeds, of which 388 had colored and 567 colorless aleurone. This obviously approaches closely a 27 : 37 ratio, the percentage of colorless seeds being 59.4 ± 1.1 while the theoretical percentage is 57.8 (Emerson, 1918). The deviation from expectation, 1.6 ± 1.1 per cent, is such as might be expected by chance once in three trials, P equaling 0.33. Evidently, therefore, the aleurone factors A, C, and R are concerned in these crosses. Since A and R are assumed by the hypothesis to be plant-color factors also, there is afforded opportunity of comparing the plant-color classes from colored with those from colorless seeds. Since colored aleurone requires the interaction of A, C, and R, colored seeds should never produce brown plants nor green plants of type VI, both of which are $a\ a$. As seen from the data given below, no brown plants came from colored seeds but a few wholly green plants appeared. Greens of type IVg are of course to be expected from seeds homozygous for R^g. Owing to the fact that a larger percentage of colorless than of colored seeds produced plants; the theoretical distribution with respect to plant color, given below, was calculated separately for colored and for colorless seeds. For the colored seeds there are nearly two chances in

five (P equaling 0.58), and for the colorless seeds only about one chance in fourteen (P equaling 0.07), that the observed deviations may be due to errors of random sampling. The comparisons follow:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI	Total
Colored seeds:							
Observed	148	51	25	8	0	23	255
Calculated	143	48	32	11	0	21	255
Difference	+5	+3	—7	—3	0	+2	0
Colorless seeds:							
Observed	161	49	42	11	88	75	426
Calculated	136	45	39	13	104	89	426
Difference	+25	+4	+3	—2	—16	—14	0

It is noteworthy that the ratio of purples and sun reds to dilute purples and dilute sun reds is considerably greater for plants grown from colored seeds than for those from colorless seeds. This is to be expected from the fact that R must be present in all colored seeds, while some of the colorless seeds here concerned were doubtless $r\, r$. Hence, $R^g\, R^g$ should have occurred more frequently in the colored than in the colorless seeds, and should, by the hypothesis here under test, have reduced the numbers of dilute purples and dilute sun reds, causing these plants to appear as greens, types IIIg and IVg. If the 23 green plants grown from colored seeds are added to the dilute purples and dilute sun reds, the ratio of strong to dilute purples and sun reds approaches closely the ratio observed for the plants from colorless seeds.

It is even more instructive to note the relation of aleurone color to plant color in the case of the three F_2 lots for which anther colors were recorded (table 36, page 146). For this comparison the few purple and sun red plants whose anther colors were not recorded have been distributed to the colored-anther and green-anther classes in approximately the ratio in which these anther colors were found to occur in the cases in which anther colors were recorded. Since a larger proportion of colorless than of colored seeds produced plants, the theoretical distribution has been calculated separately for the two classes of seeds. The comparisons follow:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Colored aleurone:									
Observed......	48	25	11	12	16	4	0	10	126
Calculated.....	47	24	16	8	16	5	0	10	126
Difference.....	+1	+1	—5	+4	0	—1	0	0	0
Colorless aleurone:									
Observed......	78	11	23	4	23	6	42	40	227
Calculated.....	62	10	21	4	21	7	55	47	227
Difference.....	+16	+1	+2	0	+2	—1	—13	—7	0

In view of the rather large number of plant-color classes and the comparatively small number of individuals concerned here, the fit of the observed to the theoretical distribution is remarkably good. The deviations are such as might be expected by chance seven times in ten trials for the colored-seeded lot ($P = 0.70$), and about once in four trials for the colorless-seeded lot ($P = 0.26$). In addition to this comparison of the lot as a whole, it should be noted that, while among the purple and sun red plants as a whole the expected relation of colored (purple and pink) anthers to colorless (green) anthers is 3:1, for the colored-seeded lot it is 2:1 and for the colorless-seeded lot it is 6:1. The observed relations were 59:37 and 101:15, or about 1.6:1 and 6.7:1, respectively. On the whole, therefore, this comparison, involving aleurone color as well as plant color, supports the suggested factorial interpretation.

Later behavior of F_2 purple I.— Only three F_2 purples with purple anthers were tested in F_3. One of these, 2960–9, resulted in purple plants with purple, Ia, and green, Ig, anthers, and sun red plants with pink, IIa, and green, IIg, anthers, in the respective numbers 14:9:6:3. A purple plant of the genotype $A\ A\ B\ B\ Pl\ pl\ R^g\ r^r$ should give these four classes in the relation 18:6:6:2. The observed deviations might be expected twice in five trials, P equaling 0.41.

Another F_2 purple plant, 2958–8, gave F_3 progeny consisting of the same eight color types as were seen in F_2 in table 36 (page 146). Evidently the F_2 purple plant was $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$. The deviations from expectation are such as might occur by chance in about seventeen out of any twenty such trials, P equaling 0.86. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	V	IIIg, IVg, VI	
Observed	28	13	11	3	7	3	16	11	92
Calculated	29	10	10	3	10	3	13	14	92
Difference	—1	+3	+1	0	—3	0	+3	—3	0

The third purple-anthered F_2 purple tested, 2961–3, gave in F_3 all the color types except dilute purple, IIIa, and dilute sun red, IVa. A purple plant of the genotype $A\,a\,B\,B\,Pl\,pl\,R^g\,r^r$ should give the color types observed. The observed deviations from expectation might occur by chance about once in seven trials, P equaling 0.15. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Brown	Green	Total
Anther color	Purple	Green	Pink	Green	Green	Green	
	Ia	Ig	IIa	IIg	V	VI	
Observed	37	11	5	2	12	3	70
Calculated	30	10	10	3	10	8	71
Difference	+7	+1	—5	—1	+2	—5	—1

A single green-anthered F_2 purple, 2960–7, gave four F_3 color types, purple, sun red, brown, and green, all with green anthers. This behavior is to be expected from an F_2 genotype $A\;a\;B\;B\;Pl\;pl\;R^g\;R^g$. One of the F_3 purples, 4956–1, repeated this behavior in F_4. The F_3 and F_4 progenies are shown together in the following comparison, for which $P = 0.60$:

Color types	Purple	Sun red	Brown	Green	Total
	Ig	IIg	V	VI	
Observed	84	27	35	7	153
Calculated	86	29	29	9	153
Difference	—2	—2	+6	—2	0

It is of interest to note in this connection that a plant of the genotype $A\;a\;B\;B\;Pl\;pl\;R^g\;R^g$ could not exhibit a 27:37 fatio of colored to colorless aleurone, as was the case for some of the plants dealt with earlier.

For $A\ a\ R^g\ R^r$ the aleurone-color ratio must be either 9:7 or 3:1, depending on whether the third aleurone-factor pair is $C\ c$ or $C\ C$. The F_2 purple plant 2960–7 showed a 9:7 aleurone-color ratio with 86 colored and 74 colorless seeds, $A\ a\ C\ c\ R\ R$, while the F_3 plant 4956–1 exhibited a 3:1 ratio with 213 colored and 67 colorless seeds, $A\ a\ C\ C\ R\ R$. Another purple plant of the same F_3 progeny, 4956–32, exhibited a 3:1 aleurone-color ratio and threw only green-anthered purple and sun red plants. Its genotype must have been $A\ A\ B\ B\ C\ c\ Pl\ pl\ R^g\ R^g$. Thus it is often possible, from behavior in the following generation, to know the genotype not only with respect to plant color but for aleurone color as well. This is particularly true when the B factor is present.

Of the twenty-four sorts of behavior possible, according to hypothesis, for F_2 purples of the cross under consideration, four sorts have been exhibited in F_3 and a fifth shown in F_4. This is far from an adequate study of the F_2 purples. All that can be claimed, therefore, is that, so far as they go, the results are in accord with the hypothesis.

Behavior of other F_2 color types.— Only one F_2 sun red plant with pink anthers, 2961–4, was tested in F_3. It produced sun reds with pink and sun reds with green anthers, dilute sun reds, and greens. Since anther color was noted for only a part of the plants, it has to be disregarded in classifying the F_3 progeny. The color types sun red, dilute sun red, and green occurred in the numerical relation 114:23:57. Of the eight possible genotypes of pink-anthered sun red, only three could throw these three color classes — $A\ a\ B\ b\ r^r\ r^r$, $A\ A\ B\ b\ R^g\ r^r$, and $A\ a\ B\ b\ R^g\ r^r$. From the first genotype a 9:3:4, from the second a 12:3:1, and from the third a 36:9:19, relation should exist between the F_3 classes. The poor fit of observed numbers to the 9:3:4 relation makes it improbable that the first genotype is concerned, there being only about one chance in twenty-two that the observed deviations are due to errors of random sampling, P equaling 0.045. The comparison follows:

Color types	Sun red IIa	Dilute sun red IVa	Green VIa, c	Total
Observed	114	23	57	194
Calculated	109	36	49	194
Difference	+5	−13	+8	0

A more conclusive reason for throwing out the first genotype is the fact that the plant had some seeds with colored aleurone, which would have been impossible if it were *r r*. The second genotype is discarded because of the extremely poor fit of observed numbers to the 12:3:1 relation. There is an almost inconceivably small chance that the observed deviations may be due to errors of random sampling, χ^2 equaling 180. (When $n' = 3$ and $\chi^2 = 29$, $P = 0.000001$. Higher values of χ^2 when $n' = 3$ are not listed in Pearson's tables.) The comparison follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg	
Observed	114	23	57	194
Calculated	146	36	12	194
Difference	—32	—13	+45	0

The elimination of the first two genotypes leaves the third genotype as the only one that can be concerned here. The fit of observed numbers to the 36:9:19 relation is very close, χ^2 equaling 0.84. (Values of P are not listed in Pearson's tables for values of χ^2 less than 1; when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$.) The comparison follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg, VIa, c	
Observed	114	23	57	194
Calculated	109	27	58	194
Difference	+5	—4	—1	0

This comparison leaves little doubt that the genotype of the F_2 plant concerned is $A\,a\,B\,b\,R^g\,r^r$. There are, moreover, other considerations which go far toward identifying the genotype as given here. The fact that some sun red plants of F_3 had green and others pink anthers is evidence for the constitution $R^g\,r^r$. Since dilute sun red plants appeared in F_3, there can be no question as to *B b*. The F_2 plant showed a 9:7 aleurone-color segregation, and therefore, in addition to *R r*, it must have been

either $A\,a$ or $C\,c$. An F_3 sun red plant with green anthers, $R^g\,R^g$, had 97 colored and 20 colorless seeds, again indicating either $A\,a$ or $C\,c$. If it was $A\,A\,B\,b\,C\,c\,R^g\,R^g$, both colored and colorless seeds should have given sun red and green plants in a 3:1 ratio; if it was $A\,a\,B\,B\,C\,C\,R^g\,R^g$, the colored seeds should have given sun red and the colorless ones green plants only, the plant-color ratio again being 3:1; but if it was $A\,a\,B\,b\,C\,C\,R^g\,R^g$, the colored seeds should have produced sun red and green plants in a 3:1 ratio and the colorless seeds green plants only, the ratio of sun reds to greens in the two lots together being 9:7. Actually the colored seeds resulted in 23 sun red and 10 green plants and the colorless seeds in 10 green plants only, the ratio of sun reds to greens being 23:20, thus approaching 9:7. There is, therefore, considerable assurance that the F_3 plant was $A\,a\,B\,b\,C\,C\,R^g\,R^g$, that the F_2 plant was $A\,a\,B\,b\,C\,C\,R^g\,r^r$, and that the F_3 numerical relation of plant colors was 36:9:19, as originally suggested by the closeness-of-fit test.

A single dilute purple plant of F_2, 2960–4, was tested in F_3 and found to give 38 dilute purple and 39 green plants. Of the eight possible genotypes for F_2 dilute purples, the only ones that could give only dilute purples and greens in F_3 are $A\,A\,b\,b\,Pl\,Pl\,R^g\,r^r$, $A\,a\,b\,b\,Pl\,Pl\,r^r\,r^r$, and $A\,a\,b\,b\,Pl\,Pl\,R^g\,r^r$. The first two should give a 3:1, and the third a 9:7, F_3 ratio. The plant had colored aleurone, which throws out of consideration the second genotype with $r\,r$. The F_3 plant-color ratio fits fairly well a 9:7 but not at all a 3:1 expectation, the observed numbers being 38:39 and the calculated numbers 43:34 and 58:19, with deviations of 5 and 20, and probable errors of 2.6 and 2.9, respectively. The deviation from a 9:7 ratio might occur by chance once in five trials, P equaling 0.20, but that from a 3:1 ratio not more than twice in about a million trials, P equaling 0.000002. The genotype $A\,a\,b\,b\,Pl\,Pl\,R^g\,r^r$ is therefore decidedly favored by these results. The aleurone-color record shows that this genotype is possible, since there were 57 colored and 56 colorless seeds, a relation about halfway between the 9:7 and the 27:37 ratio due to $A\,a\,C\,C\,R\,r$ and $A\,a\,C\,c\,R\,r$, respectively.

Intercrosses of F_2 color types

It is realized that the tests of F_2 types by studies of their behavior in later generations as reported above, are markedly inadequate to serve

as a demonstration of the hypothesis suggested to account for the F_2 behavior of the cross of brown, type V, with green, type IVg. It is noteworthy, however, that no results have been found that do not agree with the hypothesis. Fortunately, several intercrosses of the types found in F_2 afford additional evidence.

Purple Ig x green VIc.— Green-anthered purples, $A\ B\ Pl\ R^g$, crossed with greens of type VIc, $a\ b\ pl\ r^r$, should give F_2 results identical with those found from the original cross of brown, $a\ B\ Pl\ r^r$, with green of type IVg, $A\ b\ pl\ R^g$, since F_1 in either case should be $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$. Two such crosses are recorded in table 37, group 1 (page 146). The F_1 plants were both purple, with purple anthers. In F_2 the same eight types were noted as in F_2 of the cross of brown with green IVg (table 36). The anther color was not recorded, however, for many of the plants, so that only six color classes are shown, as in table 35. While all the expected color types are present, the fit of observed to calculated numbers is so poor that the observed deviations should not occur by chance more than once in thirty trials, P equaling 0.033. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia, g	IIa, g	IIIa	IVa	V	IIIg, IVg, VI	
Observed....	80	13	9	9	20	27	158
Calculated...	66	22	17	6	22	25	158
Difference...	+14	—9	—8	+3	—2	+2	0

If, notwithstanding the poor fit shown above, the F_1 was $A\ a\ B\ b\ Pl\ pl\ R^g\ r^r$, a backcross of F_1 with green of type VIc, $a\ b\ pl\ r^r$, should result in the same six major plant-color types, but no green-anthered purples or sun reds should occur. Such crosses are listed in group 2 of table 37. All the purple plants had purple anthers and all the sun red plants had pink anthers. Moreover, the six color classes appeared in so very nearly the expected relation of 1:1:1:1:1:3 that deviations as great as those observed might be expected to occur by chance perhaps ninety-nine times in one hundred trials, x^2 equaling 0.85 (when $x^2 = 1$ and $n' = 6$, $P = 0.96$). The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Brown	Green	Total
	Ia	IIa	IIIa	IVa	V	VI	
Observed.......	36	29	31	31	31	95	253
Calculated......	31.6	31.6	31.6	31.6	31.6	94.9	252.9
Difference......	+4.4	—2.6	—0.6	—0.6	—0.6	+0.1	+0.1

If an F_1 supposedly $A\,a\,B\,b\,Pl\,pl\,R^g\,r^r$, be backcrossed to dilute sun red, type IVa, $A\,b\,pl\,r^r$, color types Ia, IIa, IIIa, and IVa should appear, none of them with green anthers. Such crosses are presented in group 3 of table 37. The anthers thruout were purple or pink, and the several color types appeared in approximately equal numbers, as expected, there being more than two chances in five that the observed deviations may have been due to errors of random sampling, P equaling 0.42. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed...............	115	97	95	111	418
Calculated..............	104.5	104.5	104.5	104.5	418
Difference..............	+10.5	—7.5	—9.5	+6.5	0

If the same F_1 genotype, $A\,a\,B\,b\,Pl\,pl\,R^g\,r^r$, be backcrossed with green of type IVg, $A\,b\,pl\,R^g$, there should occur five major color types, brown not appearing, and both green and colored anthers should be found in both the purple and the sun red plants. The records of such a cross are given in group 4 of table 37. The seven expected color types occurred in numbers near enough to expectation so that there are nearly three chances in ten that the deviations may have been due to errors of random sampling, P equaling 0.29. The most pronounced deviations are the excess of dilute sun reds and the deficiency of greens. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	IIIg, IVg	
Observed	10	13	7	8	10	15	13	76
Calculated...............	9.5	9.5	9.5	9.5	9.5	9.5	19	76
Difference...............	+0.5	+3.5	—2.5	—1.5	+0.5	+5.5	—6	0

In conclusion it seems safe to say that the cross of green-anthered purple, Ig, with green of type VIc, has given results similar to those yielded by the cross of brown, V, with green of type IVg. Since this was to have been expected from the hypothesis suggested by the F_2 generation of the latter cross, the results just discussed lend support to that hypothesis.

Purple Ig x dilute sun red IVa.— In accordance with the hypothesis under consideration, green-anthered purple is $A\ B\ Pl\ R^g$ and dilute sun red is $A\ b\ pl\ r^r$. F_1 of the cross should be $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, and F_2 should consist of the five major color types, purple, sun red, dilute purple, dilute sun red, and green of types IIIg and IVg, with both green-anthered and colored-anthered subclasses of purples and sun reds. The F_1 plants were purple-anthered purples, as expected. Three F_2 progenies are recorded in table 38, group 1. Anther color could not be recorded in all cases, but in each of the three F_2 progenies both green and colored anthers were noted for both purple and sun red plants. In one progeny, 5042–5045, of a total of 57 purples and sun reds, 41 had colored and 16 had green anthers, which is not far from the expected 3:1 relation. The 415 F_2 plants were so distributed among the five color classes that the chances are nearly three in five that the deviations observed may have been due to errors of random sampling, P equaling 0.58. A comparison of observed and theoretical distributions follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Green	Total
	Ia, g	IIa, g	IIIa	IVa	IIIg, IVg	
Observed	243	71	59	22	20	415
Calculated	234	78	58	19	26	415
Difference	+9	—7	+1	+3	—6	0

An F_1 of the cross here considered, 6557–12, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, was backcrossed to a dilute sun red, $A\ b\ pl\ r^r$. Four color types occurred in the progeny, as expected, and all the plants had colored anthers. The deviations from expectation were such as might occur by chance in considerably more than one out of any two such trials, P equaling 0.56. The comparison follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Total
	Ia	IIa	IIIa	IVa	
Observed	43	43	35	48	169
Calculated	42	42	42	42	168
Difference	+1	+1	−7	+6	+1

Purple Ia x green IVg.— The cross between purple Ia and green IVg should have given results identical with those expected from the cross of green-anthered purple with dilute sun red. The parents are supposed to have been $A\ B\ Pl\ r^r$ and $A\ b\ pl\ R^g$, and the F_1, therefore, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$. The F_1's were purple-anthered purples. Two F_2 progenies are listed in table 38, group 2. All the expected color types occurred, but the observed frequency distribution was such as might be expected to occur by chance only about once in eleven trials, P equaling 0.09. If these progenies are grouped into five classes, anther color being disregarded, the fit is somewhat better, P equaling 0.16. The comparison of observed and theoretical frequencies follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute sun red	Green	Total
Anther color	Purple	Green	Pink	Green	Purple	Pink	Green	
	Ia	Ig	IIa	IIg	IIIa	IVa	IIIg, IVg	
Observed	26	14	17	3	9	2	1	72
Calculated	31	10	10	3	10	3	5	72
Difference	−5	+4	+7	0	−1	−1	−4	0

The F_2 of this cross exhibited, as expected, practically the same results as were obtained from the cross of green-anthered purple with dilute sun red. Unlike that cross, the one under consideration here was checked by the behavior of some of its F_2 types in later generations.

A single F_2 purple-anthered purple produced in F_3 16 plants (table 39, group 1), including only purple, sun red, and dilute purple in the relation 9:4:3. Of both the purples and the sun reds, some plants had colored and some had green anthers. Obviously two other types, dilute sun red and green, should occur in such an F_3 and doubtless would have been found had a larger number of plants been grown, for the F_2 plant, in order to have produced the color types recorded, must have been $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$.

Only one plant of each of the missing classes was to have been expected, and the distribution as a whole was not far from expectation, P equaling 0.59. Both the types lacking in F_3 occurred in F_4, a pink-anthered sun red F_3 producing sun reds and dilute sun reds, while green-anthered purples produced in one instance purples, sun reds, and greens, and in another instance purples and greens only, all with green anthers. This F_3 lot may consequently be regarded as $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$, and therefore equivalent to the F_2 lot from which it came, and its F_4 progenies equivalent to F_3 progenies.

A second F_2 purple-anthered purple was backcrossed to green plants of types IVg and VIc (group 1, table 39). From the backcross with green of type IVg, $A\ b\ pl\ R^g$, five major color types appeared and both the purple and the sun red types contained subtypes with colored and with green anthers. While all the classes expected from an F_2 of the genotype $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$ occurred, the frequency distribution was so far from expectation that there is only one chance in five hundred that the observed deviations may have been due to errors of random sampling, P equaling 0.002. The expected and observed distributions are as follows:

Color types	Purple	Sun red	Dilute purple	Dilute sun red	Green	Total
	Ia, g	IIa, g	IIIa	IVa	IIIg, IVg	
Observed	15	15	5	1	9	45
Calculated	9	9	9	9	9	45
Difference	+6	+6	—4	—8	0	0

Whether the discrepancy is genetically significant or was due to some accident of pollination cannot now be determined. A backcross of the same F_2 plant with green of type VIc, $a\ b\ pl\ r^r$, yielded only four color types, as expected (group 1, table 39), the anthers being colored in all cases. The excess of purples and deficiency in two other classes makes the deviations from expectation fairly great, so that there is only about one chance in seven that they may have been due to errors of random sampling, P equaling 0.14. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	27	19	15	14	75
Calculated	19	19	19	19	76
Difference	+8	0	—4	—5	—1

A third purple-anthered purple, an F_3 plant of the lot regarded as equivalent to F_2's, gave in the next generation purple-anthered purples and pink-anthered sun reds in the relation 31:7 (group 2, table 39). From the genotype $A\,A\,B\,B\,Pl\,pl\,r^r r^r$, these two phenotypes should appear in a 3:1 ratio. The deviation from expectation was 2.5 ± 1.8, or only such as might be expected about once in three trials, P equaling 0.34.

Two green-anthered purples of F_2 and two of the equivalent F_3 lot noted above were tested by a later generation. Two of the four yielded three color types, purple, sun red, and green, all with green anthers (group 3, table 39). Such behavior is expected from the genotype $A\,A\,B\,b\,Pl\,pl\,R^g\,R^g$. The 9:3:4 relation is approached so closely that the value of P cannot be determined from Pearson's tables, x^2 equaling 0.36. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	37	11	14	62
Calculated	36	12	16	64
Difference	+1	—1	—2	—2

The same two green-anthered purples were backcrossed with green of type IVg, and one of them and a sib of the other with green of type VIc, with results as shown in group 3 of table 39. The crosses with type IVg, $A\,b\,pl\,R^g$, gave the same three classes as did the self-pollinations, and the frequency distribution differed from expectation by values that might occur by chance about once in two trials, P equaling 0.49. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	34	32	53	119
Calculated	30	30	60	120
Difference	+4	+2	—7	—1

The backcrosses of these green-anthered purples with green of type VIc, $a\ b\ pl\ r^r$, as was to be expected, gave very different results. There were produced four instead of three phenotypes, all with colored (purple or pink) instead of green anthers. The deviations from the theoretical frequency distribution are such as might be expected about once in five trials, P equaling 0.21. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	44	48	33	52	177
Calculated	44	44	44	44	176
Difference	0	+4	—11	+8	+1

The other two green-anthered purples that were tested yielded only two phenotypes, green-anthered purple and green, in the relation 56:18 (group 4, table 39). The genotype $A\ A\ B\ b\ Pl\ Pl\ R^g\ R^g$ should give these two phenotypes in a 3:1 ratio. The deviation from expectation was therefore 0.5 ± 2.5. One of the same plants backcrossed to green of type IVg gave 28 green-anthered purples and 27 greens where equality was expected.

Of the twelve kinds of behavior expected of F_2 purples of the cross of purple-anthered purple with green IVg, only four have been demonstrated. So far as they go, however, the results are quite in accord with the hypothesis under test. In addition to the F_2 purples, sun reds and dilute purples also were tested by later generations, as detailed below.

Three pink-anthered sun reds gave sun reds and dilute sun reds only, all with pink anthers (table 40, group 1). These three plants are therefore regarded as $A\ A\ B\ b\ pl\ pl\ r^r\ r^r$. The ratio observed was 97:26. The deviation from the expected 3:1 ratio was 4.75 ± 3.24, or such as might

occur by chance once in three trials, P equaling 0.32. One of these three sun reds, when crossed with a dilute purple, $A\ b\ Pl\ r^r$, gave 71 purples and 77 dilute purples, all with purple anthers, where equal numbers were expected.

Three other F_2 pink-anthered sun reds produced nothing but sun red plants in F_3, 228 in all (group 2, table 40). Some plants of each progeny had pink and some had green anthers. Small plantings of each lot were made in the garden and larger plantings in the field. Anther color was noted in the case of the garden plants only. The records show 44 with pink and 16 with green anthers, a deviation from a 3:1 ratio of only 1.0 ± 2.3. The F_2 sun reds are therefore assumed to have been $A\ A\ B\ B\ pl\ pl\ R^g\ r^r$. One of these F_2 plants was backcrossed to green, both of type IVg and of type VIc, resulting in a total of 108 sun red plants (group 2). Altho no counts were made for anther color, it was noted that the cross with green IVg, $A\ b\ pl\ R^g$, gave both pink- and green-anthered plants, while the cross with green VIc, $a\ b\ pl\ r^r$, gave pink anthers alone. Only two of the six possible genotypes of F_2 sun reds were demonstrated.

Only one dilute purple F_2 plant was tested further (group 3, table 40). From self-pollination it yielded 46 dilute purple and 9 dilute sun red plants, all with colored (purple or pink) anthers. The deviation from a 3:1 ratio, 4.75 ± 2.17, is such as might be expected by chance about once in seven trials, P equaling 0.14. The same F_2 plant when backcrossed to green of types IVg and VIc (group 3) gave 85 dilute purples and 82 dilute sun reds where equality was expected. Evidently this F_2 was $A\ A\ b\ b\ Pl\ pl\ r^r\ r^r$.

No F_2 dilute sun red or green plants were tested further. One F_3 dilute sun red, however, was found to breed true, producing an F_4 of 30 pink-anthered dilute sun reds. Likewise, eight F_3 and F_4 greens gave a total of 126 green plants in the next generation.

In so far as tests have been made, therefore, the cross of purple-anthered purple with green IVg has behaved as expected on the basis of the hypothetical genotype assigned to F_1, namely, $A\ A\ B\ b\ Pl\ pl\ R^g\ r^r$.

Purple Ig x green IVg.—Green-anthered purples are assumed to be $A\ B\ Pl\ R^g$, and green IVg to be $A\ b\ pl\ R^g$. The F_1 genotype is therefore, theoretically, $A\ A\ B\ b\ Pl\ pl\ R^g\ R^g$, and F_2 should consist of the three color types purple, sun red, and green, all with green anthers. Eight such F_2 progenies are recorded in table 41, group 1. The three types

occurred in so nearly the expected relation of 9:3:4 that the observed deviations might be expected by chance considerably more than once in three trials, P equaling 0.37. The comparison follows:

Color types	Purple Ig	Sun red IIg	Green IIIg, IVg	Total
Observed	293	105	150	548
Calculated	308	103	137	548
Difference	—15	+2	+13	0

The F_2 greens of this cross are assumed to consist of the genotypes $A\ b\ Pl\ R^g$ and $A\ b\ pl\ R^g$, which, if r^r had been present instead of R^g, would have been dilute purples and dilute sun reds, respectively. In substantiation of this assumption, crosses of F_1's, all green-anthered purples, with dilute sun red, $A\ b\ pl\ r^r$, and with green VIc, $a\ b\ pl\ r^r$, are recorded in group 2 of table 41. As expected, the result was the four classes purple, sun red, dilute purple, and dilute sun red, all with colored anthers. The expected numerical equality of the four classes was so closely approached that deviations such as those observed might be expected by chance in nearly three out of four trials, P equaling 0.74. The comparison follows:

Color types	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Total
Observed	58	61	62	70	251
Calculated	63	63	63	63	252
Difference	—5	—2	—1	+7	—1

Still another F_1 was crossed with a pink-anthered sun red, $A\ B\ pl\ r^r$, and gave 68 purples and 67 sun reds, all with colored anthers, where equal numbers were expected.

So far as tested, therefore, the cross of green-anthered purple with green IVg has given the results expected on the basis of the hypothesis under test.

Purple Ig x brown V.—A cross of green-anthered purple, $A\ B\ Pl\ R^g$, with brown, $a\ B\ Pl\ r^r$, gave in F_1 49 purple-anthered purples, presumably

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$A\,a\,B\,B\,Pl\,Pl\,R^g\,r^r$. An F_2 progeny was grown from only one F_1 plant, 6653–6, resulting in two major color types, purple and brown, in approximately a 3:1 ratio. The purples were, as expected, of two subtypes, one with purple and the other with green anthers. The theoretical relation of 9:3:4 was realized so closely that the observed deviations might be expected by chance in at least two out of three trials, x^2 equaling 0.76 (when $x^2 = 1$ and $n' = 3$, $P = 0.61$). The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Brown V	Total
Observed	23	5	9	37
Calculated	21	7	9	37
Difference	+2	—2	0	0

A second F_1 plant, 6653–2, was backcrossed with green IVg, $A\,b\,pl\,R^g$, resulting in 39 purple plants, 21 with purple and 18 with green anthers, where equal numbers were expected, the deviation from expectation being 1.5 ± 2.1. The same F_1 plant was crossed with a heterozygous dilute sun red, $A\,a\,b\,b\,pl\,pl\,r^r\,r^r$, resulting in 45 purple-anthered purples and 18 browns, the deviation from the expected 3:1 ratio being 2.25 ± 2.32.

Purple Ig x dilute purple IIIa.— Crosses of green-anthered purple, $A\,B\,Pl\,R^g$, with dilute purple, $A\,b\,Pl\,r^r$, gave in F_1 purple-anthered purple, $A\,A\,B\,b\,Pl\,Pl\,R^g\,r^r$. The F_2 should consist of purple-anthered and green-anthered purples, dilute purples, and greens, the three major color types appearing in the relation 12:3:1. In F_2 from a single F_1 plant, 5263–3, both purple-anthered and green-anthered purples were noted, but detailed counts based on anther color were not made. The deviations from the expected numbers for the three major types were such as might occur by chance in nine out of twenty such trials, P equaling 0.45. The comparison follows:

Color types	Purple Ia, g	Dilute purple IIIa	Green IIIg	Total
Observed	36	11	5	52
Calculated	39	10	3	52
Difference	—3	+1	+2	0

A second F_1 plant backcrossed with green IVg, $A\ b\ pl\ R^g$, gave the expected four types. The deviations from the equal frequency expected for the several types was such as might occur by chance somewhat more than once in four trials, P equaling 0.27. The comparison follows:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Dilute purple IIIa	Green IIIg	Total
Observed...	59	67	80	77	283
Calculated..	71	71	71	71	284
Difference..	—12	—4	+9	+6	—1

Dilute purple IIIa x green IVg.—A single cross of dilute purple, $A\ b\ Pl\ r^r$, with green IVg, $A\ b\ pl\ R^g$, gave dilute purple, $A\ A\ b\ b\ Pl\ pl\ R^g\ r^r$, in F_1, and three phenotypes, dilute purple, dilute sun red, and green, in F_2 (table 42, group 1, page 150). The observed frequencies were 23:8:10, which is the nearest possible approach to the expected 9:3:4 relation for a total of 41 individuals. One F_2 dilute purple gave similar results in F_3, indicating the same genotype as the F_1 dilute purples. The F_4 progenies of this F_3 lot may be regarded as equivalent to F_3's, and are therefore grouped with the F_3 in table 43. Three F_3 and F_4 progenies (table 43, group 1A) approached the 9:3:4 relation so closely that the observed deviations might occur by chance in nearly three out of five trials, P equaling 0.59. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed..................	143	48	73	264
Calculated................	149	50	66	265
Difference................	—6	—2	+7	—1

The green plants of these F_3 and F_4 lots, as well as those of the F_2 lot listed in group 1 of table 42, are assumed to be $A\ b\ Pl\ R^g$ and $A\ b\ pl\ R^g$, and consequently to differ from the dilute purples and dilute sun reds only in having $R^g\ R^g$ in place of $R^g\ r^r$ or $r^r\ r^r$. That the $R\ r$ pair is thus concerned in these results can be shown by a comparison between the plant-

color phenotypes resulting from seeds with colored aleurone and those from seeds with colorless aleurone. The F_2 progeny came from a plant that produced from self-pollination colored and colorless seeds in the relation 60:24. This close approach to a 3:1 ratio indicates that the F_1 plant could have been heterozygous for only one of the aleurone-factor pairs *A a*, *C c*, or *R r* (Emerson, 1918). A cross with a *C* tester, *A c R*, resulted in 43 colored and no colorless seeds, while a cross with an R tester, *A C r*, gave 46 colored and 32 colorless seeds, thus indicating *R r* as the factor pair concerned. The colorless seeds must therefore have been *r r*, presumably $r^r\ r^r$, and in accordance with the hypothesis under test should have produced no green plants. Some of the colored seeds, on the contrary, should have been *R R*, supposedly $R^g\ R^g$, and these should have given green plants. For the most part, the colored and the colorless seeds were planted separately. The 9:3:4 relation of the three plant-color types is theoretically made up of a 6:2:4 relation from colored seeds and a 3:1:0 relation from colorless seeds. Actually, from colorless seeds there appeared dilute purple and dilute sun red plants in the ratio 69:15. The deviation from expectation, 6.0 ± 2.7, might be expected to occur about once in seven trials, P equaling 0.14. From colored seeds the deviation from the theoretical distribution was such as might occur thru errors of random sampling almost once in four trials, P equaling 0.23. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	92	42	70	204
Calculated	102	34	68	204
Difference	—10	+8	+2	0

Aleurone is in some cases self-colored and in some cases mottled. Mottled aleurone ordinarily occurs only when the *R* factor is heterozygous, but not all heterozygous individuals are mottled (Emerson, 1918). Mottled seeds of the cross under discussion, just as colorless ones, since they are presumably $R^g\ r^r$, should produce no green plants. In the case of some of the progenies noted above, the colored seeds were sorted into self-colored, mottled, and colorless. Since usually about one-third

of the colored seeds are mottled, the 9:3:4 relation of plant-color types observed in this cross should be made up of a 3:1:0 relation from colorless seeds, 3:1:0 from mottled seeds, and 3:1:4 from self-colored seeds. Of the progenies for which the seeds were sorted in this way, the colorless seeds produced dilute purple and dilute sun red plants in the relation 60:14, with a deviation from 3:1 of 4.5 ± 2.5, the mottled seeds gave the same plant-color types in the relation 30:12, with a deviation of 1.5 ± 1.9, and the self-colored seeds yielded dilute purple, dilute sun red, and green in the relation 48:19:64 (the theoretical distribution for a total of 131 individuals is 49:16:66), the deviations being such as might occur by chance perhaps three times in four trials, χ^2 equaling 0.64. On the whole, therefore, these crosses, and particularly the interrelations of aleurone and plant colors, afford strong evidence in support of the hypothesis under test.

Before presenting further F_3 results from these crosses, it may be well to consider other crosses of dilute purple with green IVg which, so far as plant color alone is concerned, have given results quite like those presented above but which exhibit a wholly different relation between plant color and aleurone color. The green plants concerned in these other crosses were C testers for aleurone color (Emerson, 1918), and were therefore known to be $A\ c\ R$, presumably $A\ c\ R^g$. The dilute purple plants concerned were homozygous for aleurone color, and were consequently $A\ C\ R$, presumably $A\ c\ R^r$. These crosses differ, then, from the ones discussed above in having R^r in place of r^r and c in place of C. Since the $C\ c$ pair is supposed not to have any relation to plant color, the results for plant color should be quite like those for the other cross and there should be no relation between plant color and aleurone color. The results for F_2 are presented in table 42, group 2, and the F_3 results in table 43, group 1B. The three plant-color types appeared in F_2 in the relation 328:113:148, and in F_3 in the relation 40:14:23. Considered together these lots deviated very slightly from expectation, χ^2 equaling 0.31. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Observed	368	127	171	666
Calculated	375	125	166	666
Difference	−7	+2	+5	0

The seeds from which these plants were grown consisted of colored and colorless in approximately a 3:1 ratio, as is expected when the C factor alone is heterozygous. The deviations from the expected 9:3:4 relation for plants from colored seeds was such as might occur by chance more than once in three trials, P equaling 0.36, and for plants from colorless seeds such as might occur once in six trials, P equaling 0.17. The comparisons follow:

Plant-color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg	Total
Colored seeds:				
Observed	215	58	89	362
Calculated	204	68	90	362
Difference	+11	—10	—1	0
Colorless seeds:				
Observed	65	32	32	129
Calculated	73	24	32	129
Difference	—8	+8	0	0

The results presented for plant color alone and in relation to aleurone color in these crosses are therefore quite in keeping with the hypothetical constitution assigned to the F_1 plants, namely, $A\,A\,b\,b\,Pl\,pl\,R^r\,R^g\,C\,c$, just as the results from the other crosses were in keeping with the assumed genotype $A\,A\,b\,b\,Pl\,pl\,R^g\,r^r\,C\,C$ for their F_1 plants.

A single F_1 plant was backcrossed with green IVg, $A\,b\,pl\,R'$, with results as shown in table 42, group 3. The three color types dilute purple, dilute sun red, and green, occurred in the relation 46:45:86. The expected distribution for a total of 177 individuals is 44:44:89, showing almost a perfect fit, x^2 equaling 0.21.

For both the lots of crosses under discussion, further tests are afforded by the behavior in F_3 and F_4. As already shown, some of the F_2 dilute purples had the same genetic constitution as the F_1 plants (table 43, groups 1A and 1B). The progenies of two other dilute purples, one of F_2 and the other of an equivalent F_3, produced dilute purple and dilute sun red plants only (group 2, table 43), in the relation 82:23. The devia-

tion from a 3:1 ratio is 3.25 ± 2.99. From their behavior and in view of the crosses in which they occurred, one of these plants is assumed to have been $A\ A\ b\ b\ Pl\ pl\ r^r\ r^r$ and the other $A\ A\ b\ b\ Pl\ pl\ R^r\ R^r$.

A single dilute purple of an F_3 lot equivalent to an F_2 gave dilute purple and green plants only (group 3, table 43). The two color types appeared in the ratio 62:16, a deviation from 3:1 of 3.5 ± 2.6. The F_3 plant is therefore assumed to have been $A\ A\ b\ b\ Pl\ Pl\ R^g\ r^r$. Colorless and mottled seeds produced dilute purple plants only, as was expected. From self-colored seeds there resulted dilute purple and green plants in the relation 26:16, a deviation of 2.0 ± 2.0 from the expected 2:1 ratio.

Two dilute sun red plants gave progenies of dilute sun reds and greens in the relation 63:22, a deviation from a 3:1 ratio of 0.75 ± 2.69 (group 4, table 43). Presumably these plants were $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$ and $A\ A\ b\ b\ pl\ pl\ R^r\ R^g$. Four other dilute sun red plants bred true in the next generation (group 5, table 43), producing a total of 197 dilute sun red plants. These plants are therefore assigned the genotype $A\ A\ b\ b\ pl\ pl\ r^r\ r^r$.

Seven green plants likewise bred true (group 6, table 43), producing a total of 130 green plants. These plants were presumably $A\ b\ pl\ R^g$ and $A\ b\ Pl\ R^g$.

To summarize, all types of behavior were observed in F_3 and equivalent F_4 generations of the cross of dilute purple with green IVg except true-breeding dilute purples. Only eight dilute purples were tested, and only one in nine is expected to breed true.

Sun red IIg and IIa and dilute sun red IVa x green IIIg and IVg.— Two crosses of green-anthered sun red with green IVg gave green-anthered sun red plants in F_1, theoretically $A\ A\ B\ b\ pl\ pl\ R^g\ R^g$. The parent types only appeared in F_2 (table 44, group 1). The observed numbers of green-anthered sun reds and greens were, respectively, 216 and 77. The deviation from the expected 3:1 ratio was 3.75 ± 5.00.

A cross of pink-anthered sun red with green IVg gave pink-anthered sun red in F_1, theoretically $A\ A\ B\ b\ pl\ pl\ R^g\ r^r$. F_1 plants backcrossed with green IVg, $A\ b\ pl\ R^g$, gave three major plant-color types (group 2, table 44) — sun red, dilute sun red, and green — with the sun reds appearing in two subtypes, one pink-anthered and the other green-anthered. Theoretically the four types should have been represented by an equal number of individuals. The deviations from this expectation were such

that there is considerably more than an even chance that they might have been due to errors of random sampling, P equaling 0.56. The comparison follows:

Color types	Sun red, pink anthers IIa	Sun red, green anthers IIg	Dilute sun red IVa	Green IVg	Total
Observed.........	105	90	105	109	409
Calculated........	102	102	102	102	408
Difference........	+3	—12	+3	+7	+1

Crosses of dilute sun red with green IVg gave 54 dilute sun red plants in F_1, $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$. In F_2 (group 3, table 44) there resulted from a self-pollinated F_1, dilute sun red and green plants in the relation 55:22, a deviation from the expected 3:1 ratio of 2.75 ± 2.56. An F_1 back-crossed with green IVg gave the same two color types in equal numbers, 30 each, exactly as expected. Numerous other crosses of this sort have been observed in connection with studies of the interrelations of aleurone-color and plant-color factors. Since these data are to be presented in a later paper and since they are wholly in accord with the data given in group 3 of table 44, they are not discussed here.

In an earlier section of this paper dealing with the factor pairs *A a*, *B b*, and *Pl pl* only (page 29), it was shown that the green plants there noted are of three kinds, namely, *a b pl*, *a B pl*, and *a b Pl*. Thruout the present section of the paper, which deals with the relation of the multiple-allelomorph series containing R^g, r^r, R^r, r^g, it has been assumed that plants which in the presence of r^r or R^r are dilute purple or dilute sun red, are green in the presence of homozygous R^g. The data presented are wholly in accord with this interpretation, thereby giving considerable assurance of the probable correctness of the hypothesis. The reported interrelations of plant color and aleurone color when the latter was known to involve the *R r* pair, have still further strengthened this assurance. It remains now to present even more direct evidence, namely, that obtained from crosses of green plants encountered in this study, with sun red and dilute sun red plants. These green plants are assumed to be $A\ b\ Pl\ R^g$, type IIIg, and $A\ b\ pl\ R^g$, type IVg.

Certain F_3 and F_4 progenies consisting of green-anthered purples and greens in a 3:1 relation are listed in table 39, group 4. These green plants

were all, presumably, $A\ b\ Pl\ R^g$. Green plants of a later generation, grown from these greens, when crossed with sun red plants, type IIa, gave 64 purple-anthered purples and no other types (table 45, group 1). Another green crossed with dilute sun red resulted in 4 dilute purples. Obviously the same results would have been obtained had the green plants used in these crosses been $a\ b\ Pl\ r^g$, instead of $A\ b\ Pl\ R^g$ as they are supposed to have been. As a matter of fact, however, one of these green plants had homozygous colored aleurone, and therefore must have been $A\ C\ R$. The other two greens, while they had colorless aleurone, came from lots known, from their 3:1 aleurone-color ratios and from crosses with aleurone testers, to be heterozygous for C alone, and therefore $A\ c\ R$. Moreover, the green plants from lots consisting of purples and greens in a 3:1 relation could not have been $a\ a$, for the parents of such lots, if heterozygous for A, must have produced purples and browns rather than purples and greens. The green plants could therefore have been nothing other than $A\ b\ Pl\ R^g$.

Similarly, progenies consisting of green-anthered purples and sun reds, and greens, in a 9:3:4 relation, are listed in table 39, group 3. Green plants of these lots and their green descendants might be either $A\ b\ Pl\ R^g$ or $A\ b\ pl\ R^g$, or might be heterozygous for Pl. Six such green plants were crossed with dilute sun reds (table 45, group 2). None of these greens could have been of the types discussed in the earlier section of this paper, namely, $a\ b\ Pl\ r^r$ and the like, for they were shown by appropriate tests (Emerson, 1918) to be $A\ c\ R$ and some of them have even been used as C testers for aleurone color. Two of these green plants crossed with dilute sun reds gave dilute sun reds only, 59 in all, and are consequently regarded as being $A\ b\ pl\ R^g$. Two others by similar crosses gave dilute purples and dilute sun reds in the relation 20:30, a deviation of 5.0 ± 2.4 from the expected equality from plants of the genotype $A\ A\ b\ b\ Pl\ pl\ R^g\ R^g$. Two other greens were crossed with heterozygous dilute sun reds, $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$, and gave dilute purples, dilute sun reds, and greens in the relation 69:54:106. The theoretical distribution among these three classes for a total of 229 individuals, based on the assumption that the green parent plants were $A\ A\ b\ b\ Pl\ pl\ R^g\ R^g$, is 57:57:115, a deviation that might occur by chance about once in five trials, P equaling 0.19.

Progenies consisting of dilute purples, dilute sun reds, and greens in a 9:3:4 relation are listed in table 43, group 1A. Descendants of one of

these green plants were crossed with dilute sun reds which were F_1's of crosses between dilute sun red and green IVg. The results were dilute purple and green plants in the relation 328:338 (table 45, group 3), a deviation from a 1:1 ratio of 5.0 ± 8.7. Since the heterozygous dilute sun red plants were $A\ A\ b\ b\ pl\ pl\ R^g\ r^r$, the green plants crossed with them are assumed to have been $A\ b\ Pl\ R^g$. That this assumption is correct appears the more evident from the fact that the green plants were homozygous for colored aleurone, and hence $A\ C\ R$.

Green IVg x *green VIc.*—Twelve crosses between green plants of type IVg and green plants of type VIc gave a total of 159 F_1 plants, all dilute sun red. With respect to aleurone color, all the type IVg plants concerned in these crosses were known to be $A\ c\ R$, and, in fact, were in general use as C testers for aleurone color. With respect to plant color, therefore, they are assigned the constitution $A\ b\ pl\ R^g$. Of the type VIc greens, four were known to be A testers for aleurone color, and were therefore, with respect to aleurone color, $a\ C\ R$. Their plant-color constitution is accordingly set down as $a\ b\ pl\ R^r$. Six of the type VIc greens had an aleurone-color constitution of $a\ C\ r$, their plant-color genotype being accordingly $a\ b\ pl\ r^r$. The other two VIc greens were certainly $a\ b\ pl$, but whether they were R^r or r^r is unknown.

In F_2, dilute sun red and green plants were present in the ratio 420:291 (table 46, group 1, page 154). From an F_1 of the genotype $A\ a\ b\ b\ pl\ pl$ plus $R^g\ r^r$ or $R^g\ R^r$, a 9:7 ratio of dilute sun red to green is to be expected in F_2, since both A and r^r or R^r are assumed to be necessary for the production of anthocyanic pigment, which distinguishes dilute sun red from green. The theoretical ratio for a total of 711 individuals is 400:311. The observed deviation from this ratio, 20.0 ± 8.9, is such as might occur by chance about once in eight trials, P equaling 0.13.

Two F_1 plants backcrossed to green VIc, $a\ b\ pl\ R^r$, gave 66 dilute sun red and 58 green plants, and two backcrosses with green IVg, $A\ b\ pl\ r^g$, gave 96 dilute sun reds and 96 greens, equality of the two classes being expected in the case of both crosses (group 2, table 46).

That the two parent types of green occurred in F_2 is shown by their relations to aleurone and pericarp color. In the case of every cross, green plants were produced from both colored and colorless seeds. Those from colored seeds could have been only $A\ b\ pl\ R^g$. Since some seeds were colorless because of $a\ a$ and some because of $c\ c$, both parent types of green should have been present in the lots grown from colorless seeds.

In one cross there was present the pericarp factor P, which with A gives a red and with $a\,a$ a brown pericarp. All the F_2 green plants from colored seeds had red pericarp, and of those from colorless seeds the majority had brown pericarp. From the colorless seeds there should have occurred also a combination type of green, $a\,b\,pl\,R^g$, but no tests were made for the identification of this type.

Ten dilute sun reds of F_2 were tested by their F_3 behavior. Three of these (table 47, group 1) gave dilute sun red and green plants in the relation 108:77, a deviation from a 9:7 ratio of 4.0 ± 4.6. Five other F_2 plants (group 2) gave the two color types in the relation 187:66, a deviation from a 3:1 ratio of 3.0 ± 4.6. Two F_2's (group 3) bred true dilute sun red, producing 78 dilute sun red and no green offspring. Theoretically, of 9 F_2 dilute sun reds, there should occur in F_3, true-breeding, 3:1, and 9:7 progenies in the numerical relation 1:4:4. The observed relation between these three sorts of behavior for the ten F_2's tested was 2:5:3. Deviations such as these might occur by chance about once in two trials, P equaling 0.49.

Green IVg x green VIa.—Certain crosses of green IVg with green VI have given sun red plants in F_1. The type VI greens belonged to families in which the B factor was known to be present. They were therefore doubtless $a\,B\,pl$ plus r^r or R^r, and the F_1's were probably $A\,a\,B\,b\,pl\,pl$ plus $r^r\,R^g$ or $R^r\,R^g$. F_2 consisted of the three major color types sun red, dilute sun red, and green (table 48, group 1) in the relation 586:161:348. Obviously this is not a 9:3:4 relation, for the deviations from such expectation, −30, −44, +74, could not be expected to occur thru errors of random sampling once in a million such trials, χ^2 equaling 30.9 and P equaling .000000+. As a matter of fact, an F_1 of the genotype suggested above should give in F_2 the three color types observed in the relation 36:9:19. The observed frequencies of the several classes fit this expectation so closely that the deviations from it might occur by chance in about one out of five trials, P equaling 0.19. The comparison of observed and expected frequencies follows:

Color types	Sun red	Dilute sun red	Green	Total
	IIa, g	IVa	IVg, VIa, c	
Observed	586	161	348	1,095
Calculated	616	154	325	1,095
Difference	—30	+7	+23	0

Not only were the frequencies of the major color types fairly close to expectation, as indicated above, but the expected subclasses of sun red with pink anthers and with green anthers were observed. Counts of anther color were made in the case of only 65 individuals. These plants were distributed to the four color classes, pink-anthered sun red, green-anthered sun red, dilute sun red, and green, in the order 24:9:10:22. The theoretical distribution of 64 individuals being 27:9:9:19, the deviations are such as might occur by chance perhaps twice in three trials, χ^2 equaling 0.91 (when $\chi^2 = 1$ and $n' = 3$, $P = 0.61$).

Only three F_2 sun reds were tested in F_3. One of them (group 2, table 48) bred true sun red, but segregated with respect to anther color. It was therefore presumably $A\ A\ B\ B\ pl\ pl\ r^r\ R^g$. Two other F_2 sun reds (group 3) gave sun red and green offspring in the ratio 229:71, a deviation of only 4.0 ± 5.1 from a 3:1 ratio. One of these two F_2 plants was crossed with a dilute sun red, resulting in 55 sun red plants. The two F_2 plants, therefore, were presumably $A\ a\ B\ B\ pl\ pl$. Anther color was not determined, but the fact that the green plants of F_3 all came from colorless seeds is conclusive evidence for the presence of $A\ a$ and against the presence of $r^r\ R^g$. The genotype of the F_2 plants is accordingly set down as $A\ a\ B\ B\ pl\ pl\ r^r\ r^r$.

Green IIIg x green VIc.— Green plants known to be of type VIc, $a\ b\ pl\ r^r$, were crossed with greens which were known to be $R^g\ R^g$ and which from their parentage might have had Pl. The result in F_1 was dilute purple, supposedly $A\ a\ b\ b\ Pl\ pl\ r^r\ R^g$. Two F_2 lots (table 49, group 1) consisted of dilute purples, dilute sun reds, and greens in the relation 109:37:135. From the assumed genotype of F_1, there should occur in F_2 the observed color types in the relation 27:9:28. The observed frequencies deviated from the theoretical ones by amounts such as might occur by chance once in three trials. P equaling 0.33. The comparison follows:

Color types	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c	Total
Observed	109	37	135	281
Calculated	119	40	123	282
Difference	—10	—3	+12	—1

The dilute purples of F_2 were presumably all $A\ b\ Pl\ r^r$ and the dilute sun reds all $A\ b\ pl\ r^r$. Of the F_2 greens there should theoretically have been six types, namely, $A\ b\ Pl\ R^g$, $A\ b\ pl\ R^g$, $a\ b\ Pl\ r^r$, $a\ b\ pl\ r^r$, $a\ b\ Pl\ R^g$, and $a\ b\ pl\ R^g$. The relation of these plant colors to aleurone color and to a pericarp color known as cherry, present in these families, affords an opportunity of checking some of these hypothetical formulae. Cherry pericarp is a bright reddish purple, somewhat variable in intensity. In the parent of one of these F_2 progenies it was sufficiently light to make possible the determination of the underlying aleurone color. The F_2 seeds consisted of colored and colorless aleurone in the ratio 140:171, a deviation from a 27:37 ratio of 9.0 ± 5.9, or such a deviation as might occur by chance three times in ten trials, P equaling 0.30. The F_1 plants were known to be $A\ a\ R\ r$, and in order to give a 27:37 ratio with respect to aleurone color they must have been also $C\ c$. Cherry pericarp is of such a nature that it never develops except in the presence of *Pl*. With *A* and *Pl* it is cherry, but with *a* and *Pl* it is brownish. It had been regarded by the writer as due to a factor, *Ch*, but recently Dr. E. G. Anderson has shown (by unpublished data) that the writer's *Ch* is apparently another allelomorph of *R*, and at present it is known to exist only in the form r^{ch}. Since all dilute purples of the lots under consideration here are assumed to be $A\ b\ Pl\ r^{ch}$, they should all have cherry pericarp. Again, since dilute sun reds are $pl\ pl$, they should all have colorless pericarp. Furthermore, since all green plants from colored seeds are supposed to be $R^g\ R^g$, their pericarp should likewise be colorless. Finally, since the colorless seeds may lack color because of either $a\ a$, $r\ r$, or $c\ c$ alone, or because of both $a\ a$ and $r\ r$, some green plants from colorless seeds should have colorless pericarp, $a\ R^g$ or $A\ c\ R^g$, and some should have brownish pericarp, $a\ Pl\ r^{ch}$. Of course all green plants with $pl\ pl$ also must have colorless pericarp.

The observed results are wholly in accord with these suppositions. In one F_2 progeny, pericarp color was determined for all except a few plants. From seeds with colored aleurone, all the dilute purples had cherry pericarp and all the dilute sun reds and greens had colorless pericarp. These three classes of plant and pericarp color showed frequencies deviating from the theoretical 27:9:18 relation by quantities such as might occur by chance almost once in four trials, P equaling 0.23. From seeds with colorless aleurone, all dilute purples had cherry pericarp, all dilute sun

reds had colorless pericarp, and greens had in part brownish and in part colorless pericarp. The deviations from the expected 27:9:18:20 relation of these four color classes were such as might occur thru errors of random sampling in more than seven out of any ten such trials, P equaling 0.72. The comparisons follow:

Plant color	Dilute purple	Dilute sun red	Green	Green	Total
Pericarp color	Cherry IIIa	Colorless IVa	Brownish VIb	Colorless IIIg, IVg, VIc	
Colored aleurone:					
Observed....	43	10	0	35	88
Calculated...	44	15	0	29	88
Difference...	—1	—5	0	+6	0
Colorless aleurone:					
Observed....	38	11	32	28	109
Calculated...	40	13	27	29	109
Difference...	—2	—2	+5	—1	0

Further tests of the factorial composition, with respect to *Pl*, of some F_2 green plants of this cross are afforded by crosses between them and sun red and dilute sun red plants. One F_2 green crossed with sun red gave 27 purple plants (table 49, group 2). Since the green parent plant came from a colored seed, it is assumed to have been $Pl\ Pl\ R^g\ R^g$ plus $A\ A$ or $A\ a$. Two other greens crossed with dilute sun red gave 39 dilute purple plants, and were therefore *Pl Pl* (group 2, table 49). Since one of these green plants had brownish and the other had colorless pericarp, they are assumed to have been also r^{ch} and $R^g\ R^g$, respectively. A fourth F_2 green crossed with sun red gave purple and sun red plants, and a fifth green crossed with dilute sun red gave dilute purple and dilute sun red plants, indicating *Pl pl* (group 3, table 49). The first of these two had brownish and the second had colorless pericarp. They must therefore have been r^{ch} and $R^g\ R^g$, respectively. A sixth F_2 green crossed with dilute sun red gave only dilute sun red plants, and so must have been *pl pl* (group 4).

Green IIIg x green VIa.— In the sections immediately preceding this, it has been shown that intercrosses of greens may give dilute sun reds (page 104), dilute purples (page 106), or sun reds (page 105) in F_1, the particular color type depending on the genotypes of the greens chosen for crossing. It remains to be shown that purple Ia can be produced by intercrosses of greens. A cross of green VIa, $a B pl r^r$, with green IIIg, $A b Pl R^g$, should give this result, F_1 being $A a B b Pl pl R^g r^r$. Such a cross has been made, with results as expected.

A stock of green plants was isolated from a cross of brown V, $a B Pl r^r$, with green VIc, $a b pl r^r$, and was shown, by crosses with aleurone testers and with dilute sun red IVa, to be type VIa, $a B pl r^r$. Another lot of greens arose from a cross of purple Ig with green IVg. The purple Ig parent was from a lot consisting of purple Ia, purple Ig, dilute purple IIIa, and green IIIg, coming from a cross of purple Ig with dilute purple IIIa heterozygous for $R^g r^r$. It was therefore $A A B b Pl Pl R^g R^g$. The green IVg plant with which it was crossed was known to be $A b pl R^g$. The F_1 of this cross consisted, as was expected, of purples and greens only. The purples were type Ig and must have been heterozygous for $B b$ and $Pl pl$, and the greens must have been type IIIg and heterozygous for $Pl pl$, or $A A b b Pl pl R^g R^g$. Two of these F_1 greens were crossed with one of the greens of type VIa mentioned above. The two crosses, 9659 and 9660, resulted as expected in purple-anthered purples, type Ia, and pink-anthered sun reds, type IIa, in the relation 18:20. It has been demonstrated, therefore, that by crossing wholly green plants of appropriate genotypes it is possible to produce purple-anthered purples, the most highly colored type known, a type that is dominant to all other types.

Green IIIg x purple Ia.— A green plant with homozygous purple aleurone and belonging to a family (table 39, group 4) consisting of green-anthered purples and greens only, and therefore theoretically being $A b Pl R^g$, was crossed with a purple-anthered purple, $A B Pl r^r$. A purple-anthered purple F_1, $A A B b Pl Pl r^r R^g$, 5350–9, was backcrossed with green IVg of the genotype $A b pl r^g$, with the result that in the next generation there appeared four color types, purple-anthered purple, green-anthered purple, dilute purple, and green, in the relation 28:22:21:29. The deviations from the expected equal distribution of the 100 individuals were such as might occur by chance in considerably more than half of

such trials, P equaling 0.57. It will be recalled that results like these were obtained from a cross of green-anthered purple with dilute purple (page 96), and of course the same results were to be expected since the F_1 in both cases is supposed to have been $A\ A\ B\ b\ Pl\ Pl\ r^r\ R^g$.

The cross now under consideration has interest from the standpoint of the relation of aleurone color to plant color, and also for certain linkage relations. The F_1 was known to be, with respect to aleurone color, $A\ A\ R\ r$. Whether it was $C\ C$ or $C\ c$ was not known, since a strong red pericarp made aleurone counts impracticable. The green plant on which the F_1 was backcrossed, was determined by appropriate tests to be $C\ C$, so that the relation of the F_1 purple to C is immaterial. The backcross resulted in approximately equal numbers of seeds with and without aleurone color, there being 109 colored and 110 colorless seeds. The colorless seeds must have been $A\ B\ C\ Pl\ r^r\ r^g$ and $A\ b\ C\ Pl\ r^r\ r^g$, and should therefore have produced purple-anthered purples and dilute purples only; while the colored seeds must have been $A\ B\ C\ Pl\ R^g\ r^g$ and $A\ b\ C\ Pl\ R^g\ r^g$, and should correspondingly have produced green-anthered purples and greens only. The results were quite in accord with expectation, as is shown in the following comparison:

Color types	Purple, purple anthers Ia	Purple, green anthers Ig	Dilute purple IIIa	Green IIIg	Total
Colored seeds.....	0	22	0	29	51
Colorless seeds....	28	0	21	0	49

It has been shown earlier in this paper (page 63) that a linkage exists between the factor pair $B\ b$ and a factor pair, $Lg\ lg$, for normal or liguleless leaf, the percentage of crossing-over being about 30. It happens that the F_1 of this cross was $Lg\ lg$ as well as $B\ b$, $B\ lg$ having come from one parent and $b\ Lg$ from the other, and that the green plant used in the backcross was $b\ lg$. There is no question here that the purple-anthered purples and dilute purples produced from colorless seeds differed with respect to the $B\ b$ pair only. Their linkage with liguleless leaf, as indicated by the percentage of crossing-over, was 29.4, or a deviation from 30 of 0.6 ± 2.0. Practically the same linkage relation was found for the plants from colored seeds, green-anthered purples and greens. In this case the percentage of crossing-over was 27.5, a deviation from 30 of

2.5 ± 2.1, or such as might occur by chance about twice in five trials, P equaling 0.42. It is to be assumed, therefore, that the same difference exists between green-anthered purples and greens as between purple-anthered purples and dilute purples, namely, a difference with respect to the factor pair $B\ b$. This in turn is merely additional evidence that plants which in the presence of r^r are dilute purples, $A\ b\ Pl$, appear as greens in the presence of $R^g\ r^g$, which is the hypothesis under test thruout this section of the paper.

Purple Ia x green-anthered dilute sun red

A purple-anthered purple, known from appropriate aleurone-color tests to be $R\ R$ and hence $A\ B\ Pl\ R^r$, was crossed with a dilute sun red which differed from most dilute sun reds in showing much less anthocyanic pigment, particularly in early stages of growth, than is usual in plants of that type, and in having little, if any, color in its anthers. The F_1's, 2975, were purple-anthered purples. F_2 was expected to show the four color types, purple, sun red, dilute purple, and dilute sun red, commonly found in crosses of purple Ia with dilute sun red IVa. As a matter of fact, the single F_2 progeny grown was found to consist of these four color types as major classes, but each class was found to have colored-anthered (purple or pink) and green-anthered subclasses. The difference between the two subclasses for purple and sun red was sharp, just as is the case in crosses of purple Ia with green IVg, but it was often difficult to separate green-anthered dilute purples from green-anthered dilute sun reds. Ordinarily, anther color (purple or pink) is the surest means of distinguishing between dilute purple and dilute sun red. When both have green anthers the separation must be based on the relative amount of pigment in other plant parts — a difference that is usually not very marked until late in the life of the plants, when dilute purples usually show materially more pigment, especially in parts not exposed to the sun, than do dilute sun reds. It will be recalled that in crosses of purple Ia with green IVg, both colored and green-anthered purples and sun reds appear, but that all the dilute purples and dilute sun reds have colored anthers, the green-anthered individuals appearing as wholly green in all plant parts except perhaps the pericarp. But in the cross here considered, no wholly green plants were found.

The natural supposition is that there is here concerned still another form of the R factor, such that, while it does not allow color to develop in the anthers, does nevertheless result in the development of some anthocyanic pigment in other parts of the plant. The dilute sun red plant used as one parent of this cross was found to be $A\ c\ R$ with respect to aleurone. The factor particularly concerned in the behavior here reported is therefore assigned the designation R^{rg}. The F_1 plants are accordingly assumed to have been $A\ A\ B\ b\ Pl\ pl\ R^r\ R^{rg}$. The frequency distribution for the eight color types observed in F_2 approached the theoretical distribution so closely that deviations of the magnitude observed might occur by chance nearly three times in any ten such trials, P equaling 0.72. The comparison follows:

Plant color	Purple	Purple	Sun red	Sun red	Dilute purple	Dilute purple	Dilute sun red	Dilute sun red	Total
Anther color	Purple	Green	Pink	Green	Purple	Green	Pink	Green	
Observed...	212	77	66	22	66	23	22	3	491
Calculated.	207	69	69	23	69	23	23	8	491
Difference..	+5	+8	—3	—1	—3	0	—1	—5	0

One F_2, a green-anthered purple, was tested in F_3. This plant bred true, producing 128 green-anthered purples and no other types.

It is unfortunate that the relation of aleurone color to plant color in this cross afforded no check on the assumption that the observed behavior with respect to anther color of dilute purples and reds was due to a factor belonging to the allelomorphic series R^r, R^g, r^r, r^g. True, the F_1 plant tested was heterozygous with respect to aleurone color, but this was known to be due to $C\ c$. Since no further tests have been made, the only evidence in support of the assumption of a factor R^{rg} is the very close fit of observed with theoretical frequency distributions, the fact that colored and green anthers in purple and sun red types of many other crosses have been found to be due to the R factor, and the demonstrated presence of R in the green-anthered sun red plant used in the cross.

Summary of results involving the allelomorphic series R^r, R^g, R^{rg}, r^r, r^g, r^{ch}

Crosses of brown with green of type IVg have been shown to result in purple F_1's, and in eight color types in F_2 in a numerical relation approximating 81:27:27:9:27:9:36:40, or in six major color types, anther color being disregarded, in approximately the relation 108:36:27:9:36:40.

It has been noted that these results are wholly unlike those for crosses of brown with green reported in an earlier section of this paper, and are similar in general, tho with marked differences in detail, to previously discussed crosses of brown with dilute sun red. As an interpretation of these results, it has been assumed that, in addition to the three pairs $A\ a$, $B\ b$, $Pl\ pl$, a fourth pair — members of a multiple-allelomorph series, such as $R^r\ R^g$, $r^r\ R^g$, or $R^r\ r^g$ — is concerned. It has been assumed further that R^r or r^r is necessary ordinarily for the development of dilute purple and dilute sun red and for the appearance of purple and pink anthers in purples and sun reds, respectively, while $R^g\ R^g$ or $r^g\ r^g$ is necessary for green anthers of purples and sun reds and for the conversion of dilute purples and dilute sun reds into wholly green plants. Similarly, the appearance of green-anthered dilute purples and dilute sun reds in a single cross has been ascribed to $R^{rg}\ R^{rg}$. The relation of the R allelomorph to both aleurone color and plant color has afforded reliable tests of the hypothesis. Other tests have consisted of the behavior in later generations of the several F_2 color types and the results of intercrosses between these types. Neither of these tests has been carried to the point of exhausting all the possibilities, but in all a considerable number of tests have been made and all have given results in support of the hypothesis. A single linkage test, involving the $B\ b$ pair with leaf type, $Lg\ lg$, has afforded added support. On the whole, therefore, the hypothesis has been, if not substantiated, at least rendered highly probable.

RELATION OF ALEURONE FACTORS $C\ c$ AND $Pr\ pr$ TO PLANT COLOR

The relations of the aleurone factors A and R to plant color have been noted repeatedly in this account. A single observation suggests a relation between the aleurone-factor pair $C\ c$ and leaf color. Culture 2909 came from colored seeds of a selfed ear showing a 3:1 ratio of colored to white seeds, and therefore heterozygous for a single pair of aleurone-color factors. Several ears in the resulting progeny also gave 3:1 ratios. Tests of four plants with aleurone testers gave conclusive evidence that the $C\ c$ pair was the one concerned. One selfed plant of the lot, 2909–32, had 318 colored and 105 white seeds. Both the colored and the white seeds produced only sun red plants, some with green and some with pink anthers, indicating the genotype $A\ A\ B\ B\ C\ c\ pl\ pl\ R^r\ R^g$. All the plants showed strong sun red pigment in the sheaths and the outer husks, but

there was distinctly more red color in the leaves of the plants from colored seeds than in the leaves of the plants from white seeds. Particular attention has not been given to a possible effect of the *C* factor on mature plant colors of other color types. Many cultures of dilute sun reds and greens have afforded opportunities for observing any effect of *C* and *c* on red color in the leaves of seedlings, but no effects have been noted. No particular attention was paid to the matter at the time when the seedlings were under observation, but if the *C c* pair had exerted any marked influence it would probably have been noted.

Numerous cultures of dilute sun red seedlings have been noted with respect to possible effects of the aleurone-factor pair *Pr pr*, but no effect has been observed, the purple and the red seeds having produced seedlings with apparently the same intensity of red color. Likewise, no influence of *Pr pr* on mature plant color has ever been observed in the case of either sun red or dilute sun red. With purple and dilute purple plants, however, a distinct effect is noticeable. Purple and dilute purple plants from seeds with purple aleurone have purple anthers, while those from seeds with red aleurone have reddish purple anthers (Plate I, 1 and 3, and Plate II, 1 and 3). A similar effect is often seen also in the color of the inner husks. In neither the anthers nor the husks is the effect always sufficiently distinct to make possible an accurate separation of plants from purple and from red seeds if they are growing in mixed cultures. In some cases, however, the difference is very distinct. And when the seeds are separated with respect to purple and red aleurone, the two lots of plants resulting usually show fairly distinct differences in anther color and often in husk color as well.

EXPRESSION OF PLANT-COLOR AND ALEURONE-COLOR FACTORS

The mode of expression of the several plant-color factors has been discussed in detail in this paper, and similar discussions of aleurone-color factors are available in numerous other papers. Since aleurone colors and certain plant colors — the purple-red series — are doubtless anthocyanins, it seems natural to expect close interrelations between them. Many such relations have been noted in this account. There are certain matters, however, which need to be brought together in a summary discussion.

It will be recalled (Emerson, 1918) that for the development of any aleurone color, the presence of three dominant factors, A, C, and R, and also of a duplex recessive factor pair, $i\ i$, is necessary. The $Pr\ pr$ pair has no visible expression except when associated with this combination of the other factors, and then it determines whether the color shall be purple or red. So far as is now known, the plant-color situation with respect to complementary factors is not quite so complex. Something of the same sort is seen, however, in the fact that no anthocyanic pigment ordinarily develops except either in the presence of A and R^r, r^r, or r^{ch}, or in the presence of A, B, and $R^g\ R^g$ or $r^g\ r^g$. With the first of these combinations, the pairs $B\ b$ and $Pl\ pl$ determine the particular color type of the purple-red series. Two of these types, purple and dilute purple, are modified further by $Pr\ pr$, and the intensity of their color depends also on the member of the R series present, r^{ch} exerting a more pronounced effect than R^r or r^r. One type at least, sun red, is influenced somewhat by $C\ c$. With the second combination, A, B, and $R^g\ R^g$ or $r^g\ r^g$, the pair $Pl\ pl$ determines whether the type shall be purple or sun red. For the formation of the non-anthocyanic (flavonol) pigment, brown, the interaction of $a\ a$ with either B or Pl is essential, and usually very little color develops except when both B and Pl are present. Brown is made more intense by the presence of r^{ch}.

Of the factors concerned with plant colors of maize, the $A\ a$ pair is one of the most fundamental, since it differentiates sharply the anthocyanins of the purple-red series, $A\ B\ Pl$, $A\ B\ pl$, $A\ b\ Pl$, $A\ b\ pl$, from the non-anthocyanic brown, $a B Pl$, and the slightly brown or green $a\ B\ pl$ and $a\ b\ Pl$ and the wholly green $a\ b\ pl$. Without A no anthocyanin shows in either the aleurone or the other parts of the plant. A second fundamental pair is $Pl\ pl$, which differentiates the sun colors from those that develop in local darkness. Purple ($A\ B\ Pl$), dilute purple ($A\ b\ Pl$), and brown ($a\ B\ Pl$) are all able to develop in darkness; while sun red ($A\ B\ pl$), dilute sun red ($A\ b\ pl$), and the slight brown sometimes seen in $a\ B\ pl$, do not develop except in the presence of light. Whether or not the slight brown sometimes present in $a\ b\ Pl$ forms in darkness has not been determined. To the $Pr\ pr$ pair is due a definite qualitative difference in the colors formed which is presumably associated with a difference in chemical composition of the pigments. In the presence of Pr aleurone color is purple, and with pr it is red, and a similar difference, tho not always

so sharp a one, is seen in the effects of *Pr pr* on the anther and husk color of purples and dilute purples. The factors R^g and r^g on the one hand, both recessive with respect to plant color, and R^r and r^r on the other hand, both dominant for plant color, apparently always differentiate between colored and colorless anthers and silks in the purple-red series of plant colors, and, when *B* is absent, determine whether or not anthocyanin forms in any part of the plant. The pair *B b* influences mainly the intensity of pigmentation. Thus, purple, *A B Pl*, is more strongly colored than is weak purple, *A* B^w *Pl*, which in turn is more strongly colored than is dilute purple, *A b Pl*. The same relation holds between sun red, *A B pl*, weak sun red, *A* B^w *pl*, and dilute sun red, *A b pl*. Brown color shows very little in *a b Pl* but is strongly developed in *a B Pl*. A similar difference, however, exists between the slight brown of *a B pl* and the full brown of *a B Pl*. In the one case in which an effect of *C c* has been noted, *C* acted as an intensifier of color.

There are somewhat marked differences between the several factor pairs with respect to the stage of plant development at which their influence is expressed. Seedlings of purple, sun red, dilute purple, and dilute sun red normally exhibit no characteristic differences in intensity or extent of pigmentation. The *B b* and *Pl pl* pairs, which differentiate these color types so sharply at a later stage of growth, do not, therefore, come into expression early. All of these types are more highly colored late in their growth period than they are as seedlings, but the later changes are much more pronounced, for instance, in dilute purple than in dilute sun red, and somewhat more so in purple than in sun red. Apparently, *Pl* exerts its influence comparatively late, but under the intensifying influence of *B*, even *Pl* expresses itself fairly early.

The several factor pairs differ more or less with respect to the particular plant parts affected. Differences in the expression of *B*, B^w, and *b* are more apparent in the husks and the sheaths, particularly the upper sheaths, than elsewhere. When plants of the genotype *a B pl*, commonly classed as green, show any brown, the color is limited to the sheaths and the outer husks. The difference between purple (*A B Pl*) and sun red (*A B pl*) on the one hand, and dilute purple (*A b Pl*) and dilute sun red (*A b pl*) on the other, is more pronounced in the husks and the sheaths than elsewhere. Little difference is apparent between the two groups with respect to the color of anthers, glumes, silks, and the like. The pair

Pl pl is perhaps expressed most definitely in the color of anthers, tho the expression is by no means limited to them. Purple (*A B Pl*) and dilute purple (*A b Pl*) differ from sun red (*A B pl*) and dilute sun red (*A b pl*), not merely in having purple rather than pink anthers, but also in the coloration of their inner husks, their culms, and the like. What little brown color is seen in *a b Pl* is limited almost wholly to the staminate inflorescence. The staminate inflorescence of purples, *A B Pl*, and of browns, *a B Pl*, is strongly colored, but that of dilute purple, *A b Pl*, except for anther color, is not very different from what is seen in dilute sun red, *A b pl*. The *Pl* factor, when associated with r^{ch}, is expressed in the pericarp as cherry in purple and in dilute purple, and as brownish in brown and in green of the genotype *a b Pl*.

Factors *B b* and *Pl pl* are not known to be concerned with aleurone color. All the other factors affecting plant color are aleurone-color factors also. Of these the pair *Pr pr* influences anther color of purple and dilute purple, and to some degree the husk color as well. The pair *C c* has been observed to affect the leaf color of mature plants of the sun red type. The pair *A a* is expressed to some degree in all such parts as culms, sheaths, husks, glumes, anthers, and silks. The pericarp, if a pericarp factor *P* is present, is red with *A* and brown with *a*, or if r^{ch} and *Pl* are present, it is cherry with *A* and brownish with *a*. The *R* series of factors influences many plant parts. With duplex R^g or r^g, no color develops in any part of the plant, except the aleurone, provided *B* is absent. With *B* these factors give colorless anthers and silks merely. Factors R^r and r^r, if *A* also is present, affect practically all plant parts in which anthocyanic pigments ever develop, but are not known to have any influence on the color of the pericarp. The factor r^{ch} is, however, concerned with pericarp color provided *Pl* also is present. This factor has a marked influence on the amount of color that forms in the leaves, particularly of dilute purple and dilute sun red.

It is of no little interest that the *R* series of factors, which behaves as a group of multiple allelomorphs with regard to plant color, usually acts as a simple pair in respect to aleurone color.[6] Moreover, some of these factors act as dominants with respect to aleurone color and as recessives with respect to plant color, while the dominance of others is

[6] There is some evidence that at least one aleurone-color pattern is dependent on an allelomorph of *R r*, the three thus constituting a group of triple allelomorphs affecting aleurone-color development.

the reverse of this. For example, r^r and r^{ch} are recessive for aleurone and dominant for plant color, and R^g is dominant for aleurone and recessive for plant color, while R^r is dominant and r^g recessive for both aleurone and plant colors.

SUMMARY

In this account, six major plant-color types of maize, purple, sun red, dilute purple, dilute sun red, brown, and green (colorless), together with the subtypes, weak purple, weak sun red, green-anthered purple, green-anthered sun red, and five genotypes of green, are described and illustrated, and their environmental and genetic relations are discussed.

The sun red and dilute sun red types are shown to be dependent on light for the development of their color, while the purple, dilute purple, and brown types develop their characteristic colors in darkness. Diversities of temperature and of soil moisture are shown to have no direct effect on the formation of maize plant colors but to have an indirect relation to them thru their influence on soil fertility, which in turn bears a definite relation to the development of the purple-red series of plant color, anthocyanins, but little or no relation to brown. Sun colors particularly are shown to be markedly intensified by infertile soil. It is noted that the several types of the purple-red series are sharply differentiated when grown on fertile soil, but that their characteristic differences are largely masked by growth on infertile soil, while the brown-green series is most readily distinguished from the purple-red series, especially in the seedling stage, if grown on infertile soil. It is suggested that the effect of infertile soil may be due to a deficiency of nitrogen, and perhaps of phosphorus. Observations indicating a close connection between the accumulation of carbohydrates and strong coloration are reported, and the inference that the effect of infertile soil is brought about thru checking growth without inhibiting photosynthesis, thus allowing an accumulation of carbohydrates, is discussed.

In an attempt at a genetic analysis of the several plant-color types, data accumulated during a period of some ten years, and involving an examination of approximately 680 progenies and not less than 48,000 individual plants, are reported. As an interpretation of the results obtained from the more complex crosses, the allelomorphic pairs $A\ a$ and $Pl\ pl$, and the multiple allelomorphs B, B^w, b^s, b, and R^r, R^g, R^{rg},

r^r, r^g, r^{ch}, are assumed and genetic formulae are assigned to the several color types as follows: purple, *A B Pl*; sun red, *A B pl*; dilute purple, *A b Pl*; dilute sun red, *A b pl*; brown, *a B Pl*; green, *a B pl*, *a b Pl*, *a b pl*; all these having in addition R^r, r^r, or r^{ch}. The factor R^{rg} is assumed to be the causal factor for green anthers and silks in purple, sun red, dilute purple, and dilute sun red types, and R^g and r^g are assumed to have the same effect on purple and sun red and to insure colorlessness (green type) thruout in what would otherwise be dilute purple and dilute sun red, the *R* series having no effect on brown, except for r^{ch}, which intensifies brown as well as purple and dilute purple. Of the *R* series, R^r is dominant and r^g is recessive for both plant and aleurone color, r^r and r^{ch} are dominant for plant and recessive for aleurone color, R^g is recessive for plant and dominant for aleurone color, and R^{rg} is dominant for aleurone color and also for plant color except of the anthers and the silks, for which it is recessive. The *A a* pair is concerned with both aleurone and plant color, and the aleurone pairs *C c* and *Pr pr* are assumed to exert a modifying effect on certain plant colors.

The principal hypotheses involved are shown to be in keeping with observed facts when subjected to practically all the available genetic tests, such as backcrosses of F_1 with multiple recessives, behavior of F_2 types in later generations, intercrosses of the several F_2 types, relation of aleurone color to plant color, linkage of certain plant-color types with normal- and liguleless-leaf types and of other plant-color types with yellow and white endosperm. Approximately 32 per cent of crossing-over is reported between *B b* and *Lg lg* and about 20 to 30 per cent between *Pl pl* and *Y y*.

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APPENDIX

TABLE 1. F_1 PROGENIES OF PURPLE Ia x GREEN VIc

Pedigree nos.		Number of F_1 plants (Purple Ia)
P_1	F_1	
724–1 x 722–1	857	18
1121–8 x 1122–7	1420, 1512, 2022	40
1122–5 x 1121–2	1419, 1511	36
1525–5 x 1546–5	2056	17
Total, 4 progenies		111

TABLE 2. F_2 PROGENIES OF PURPLE Ia x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1419– 1	1513	94	22	26	12	20	23
	1511– 1	2018	61	19	13	4	13	9
	1512–12	2020	54	16	23	7	21	7
	2022– 3	4012, 4013	7	6	6	3	4	1
	2056– 6	2415, 2416, 4284	39	13	17	4	16	10
	–11	2417, 2418, 2553–2559, 4001–4007	96	22	24	3	26	8
	–16	2412, 4066, 4067	17	3	11	1	8	7
	Total, 7 progenies		368	101	120	34	108	65
2	1514–24	2054	20	7	8	1	5	2
	–31	2055	22	4	4	2	2	6
	2000– 8	2419, 4065	92	29	21	8	19	25
	2019–28	4281	24	8	4	2	4	6
	–34	4282	21	6	4	4	7	4
	2906– 1	5303	17	7	5	2	6	3
	2907– 1	5290–5293, 7050, 7051	93	26	34	7	34	23
	– 7	5299, 5300, 7054, 7055	105	46	30	10	38	31
	2981– 2	5066, 5067	17	4	5	1	8	3
	– 5	5068, 5069	20	6	2	1	2	3
	4020– 7	5712, 6810	109	44	26	12	31	33
	4032– 1	5739	16	5	3	2	3	2
	– 3	5084	15	7	5	4	4	3
	– 4	5087	13	5	4	1	7	7
	Total, 14 progenies		584	204	155	57	170	151
	Total, 21 progenies		952	305	275	91	278	216

TABLE 3. F_2 PROGENIES OF PURPLE x GREEN BACKCROSSED WITH GREEN (Ia x VIc) x VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	1420– 1 x 1430– 3	1514	12	19	15	16	14	45
	1511– 1 x 1516– 1	2019	18	8	12	8	18	50
	1512–12 x –14	2021	23	18	16	10	13	44
	2056–16 x 1995– 6	2413, 4068	4	10	8	6	8	18
	Total, 4 progenies		57	55	51	40	53	157
2	2867–69 x 4032– 1	5740	7	4	6	3	4	10
	2906– 1 x 2887–10	5305	7	5	2	8	3	9
	2907– 1 x –22	5296, 7052, 7053	10	11	10	11	9	26
	– 7 x 4032–41	5301, 5302	16	16	16	19	25	47
	4020– 7 x 2888–13	5714	2	9	9	4	4	18
	4032– 2 x 2921– 4	5094	8	6	18	12	15	33
	3 x 2888– 5	5086	19	16	21	12	18	46
	3 x 2922–16	5085	14	10	22	16	8	34
	4 x 2888– 1	5089	5	15	12	17	18	45
	4 x 2921– 4	5090–5092	25	13	19	18	15	54
	Total, 10 progenies		113	105	125	120	119	322
	Total, 14 progenies		170	160	176	160	172	479

TABLE 4. F_1 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2025–23 x 2192–14	2333, 4314	25	......	......	....
	2029– 8 x 1945–11	2304, 3596	30	......	......	....
	– 8 x 2013–19	2311	17	......	......	....
	– 8 x 2014– 8	2310, 4034	5	......	......	....
	2031–10 x 1945–10	2309	16	......	......	....
	–32 x 2012– 1	2322	20	......	......	....
	2948–16 x 4042– 2	5168, A108, A120	79	......	......	....
	4253– 2 x 4299– 2	5528, 6748A	46	......	......	1
	4305– 5 x 4042– 2	5193, 5194	24	......	......	....
	Total, 9 progenies		262	......	......	1
2	2018–69 x 2192–18	2386, 4301	30	35	......	....
	2030–13 x –14	4319	7	6	......	....
	2031–20 x 2012– 1	2325, 2326, 2543, 2544, 2950, 2951	55	55	......	....
	2043– 2 x 2026–17	2347, 4326	15	18	......	....
	2049–14 x 2192–14	2336, 4327	24	21	......	....
	2473– 3 x 2341– 1	4029	4	2	......	....
	4370– 5 x 3000– 2	4746, 4747	8	10	......	....
	Total, 7 progenies		143	147	......	....
3	2023–19 x 2192–12	2332, 4311	19	......	26	....
	–23 x –12	2330, 4310	15	......	16	....
	2027– 9 x –14	2334, 4316	15	......	18	....
	2410– 4 x 2417– 2	2993, 2994	9	......	6	....
	– 6 x – 1	2995–2998	23	......	32	....
	5500– 5 x 5130– 1	A65	24	......	25	....
	Total, 6 progenies		105	......	123	....
4	2025–10 x 2192–14	4315	1	2	6	3
	2029–27 x 2012– 1	2319, 4055	4	3	5	5
	–32 x – 1	2316, 4318	3	5	6	3
	–34 x 2014– 8	2314, 4054	1	1	2	6
	Total, 4 progenies		9	11	19	17

TABLE 5. F_2 PROGENIES OF DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
1	2310– 2..	4036, 4037.	15	7	6	3	3	7
	2332– 1..	2999, 3000.	31	9	8	1	15	7
	2950– 1..	5036, 5037.	36	12	12	2	10	9
	– 4..	5030, 5031.	37	15	13	3	8	13
	–17..	5034, 5035.	32	5	14	6	13	9
	–19..	5032, 5033.	39	12	10	3	12	5
	2995– 7..	5000–5007.	75	24	20	5	21	17
	2996– 1..	5008, 5009.	150	50	58	20	48	45
	4029– 2..	5095......	61	23	11	5	22	11
	4034– 1..	5098, 5099.	46	12	19	7	17	7
	– 2..	5104......	42	20	17	8	13	21
	5193– 1..	A135......	20	5	4	3	4	1
	5194– 5..	A136......	10	3	12	1	4	7
	5528– 8..	6748B.....	49	11	14	4	12	18
	Total, 14 progenies....		643	208	218	71	202	177
2	2973– 5..	5056–5062.	55	23	21	6	17	17
	2974– 9..	5063–5065.	75	24	23	10	18	22
	4046– 3..	5157, 5158.	20	11	6	5	7	4
	5173– 4..	A128......	19	5	8	1	9	9
	S17–19...	7762.......	35	11	5	1	14	4
	Total, 5 progenies		204	74	63	23	65	56
	Total, 19 progenies....		847	282	281	94	267	233

TABLE 6. F_2 PROGENIES OF DILUTE SUN RED x BROWN BACKCROSSED WITH GREEN (IVa x V) x VIc

Pedigree nos.		Number of F_2 plants					
F_1 x VIc	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green VIa, b, c
2310– 1 x 2411– 6..	4035.......	3	4	3	6	2	17
2922–13 x 4029– 2..	5652, 5653..	22	13	19	24	27	75
4029– 2 x 2921–10..	5096.......	9	18	12	8	13	51
4034– 1 x 2922–16..	5100–5103..	10	13	17	11	9	33
– 2 x 2921–68..	5105.......	12	5	5	4	4	16
5813–25 x 5528– 8..	6749.......	3	0	2	4	1	9
A129–12 x A108– 6..	A243, A244.	25	19	20	15	23	48
Total, 7 progenies........		84	72	78	72	79	249

TABLE 7. F_2 PROGENIES OF PURPLE x GREEN AND DILUTE SUN RED x BROWN BACK-CROSSED WITH DILUTE SUN RED

(Ia x VIc) x IVa, AND (IVa x V) x IVa

Group	Pedigree nos.		Number of F_2 plants			
	F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2056–16 x 1992–13.....	2414, 4069, 4070...	18	16	21	15
	2889–54 x 4032– 1.....	5741–5744........	24	27	21	24
	Total, 2 progenies........................		42	43	42	39
2	6730 – 9 x 6748A– 5..	7467, 7828........	87	79	75	71
	6748A–16 x 6751 –22..	7229.............	40	32	42	41
	–18 x –22..	7230.............	28	28	26	35
	–19 x – 1..	7231.............	40	33	30	36
	–20 x – 1..	7232.............	30	25	32	20
	A121– 6 x A108– 8..	A241, A242, A461, A462...........	28	25	38	45
	L188– 1 x 5528 – 8..	6786, S2..........	4	5	3	4
	Total, 7 progenies........................		257	227	246	252
	Total, 9 progenies........................		299	270	288	291

TABLE 8. F_3 PROGENIES OF SELFED AND BACKCROSSED F_2 PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
1	1513–41.........	2045, 4008, 4009.....	32	14	8	3	6	(VIa,b,c) 8
	–68.........	2048, 2475, 4010, 4011	61	14	21	7	18	10
	2018– 2.........	4268......	15	7	5	0	6	4
	– 9.........	4271......	13	8	6	1	3	3
	2020– 1.........	4275......	16	8	6	2	7	3
	4065– 6.........	5210......	9	3	3	0	1	1
	–62.........	5213......	25	7	6	2	4	1
	–63.........	5214......	22	5	5	1	12	4
	Total, 8 progenies...........		193	66	60	16	57	34
	2020-117 x 2043-11	4279......	4	4	11	4	4	18

TABLE 8 (*continued*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
2	1513 – 35	2046	11	4	6	1	.....	.....
	–138	2052	16	6	1	2	.....	.....
	2018 – 6	4270	25	9	5	5	.....	.....
	4066 – 3	5216, 5217	38	14	13	5	.....	.....
	6748B– 41	7400	12	3	4	0	.....	.....
	Total, 5 progenies		102	36	29	13	.....	.....
3								(VIa)
	1513– 59	2047	20	6	.....	.....	5	3
	– 92	2053	24	6	.....	.....	3	3
	–133	2049	16	4	.....	.....	9	2
	4037– 5	5136, 5137	35	15	.....	.....	6	7
	Total, 4 progenies		95	31	.....	.....	23	15
	2020–46 x 2200– 8	4283	5	1	.....	.....	3	3
	2411– 4 x 2412– 2	2981–2983	8	6	.....	.....	2	10
	2443– 2 x – 2	2984–2986	7	8	.....	.....	7	4
	2922–12 x 4037– 5	5138–5140	34	43	.....	.....	32	36
	Total, 4 progenies		54	58	.....	.....	44	53
4								(VIb)
	2018–27	4280	19	.....	5	.....	9	1
	2020–15	4276	19	.....	3	.....	9	3
	–30	4277	29	.....	7	.....	6	4
	4001–12	5079	11	.....	4	.....	4	1
	4005– 5	5010–5013	195	.....	77	.....	71	29
	4066– 5	5218	29	.....	12	.....	6	3
	5099–22	A78	16	.....	6	.....	6	1
	Total, 7 progenies		318	.....	114	.....	111	42
5	1513– 2	2050	19	3	.....	.....	.....	.....
	–110	2051	16	6	.....	.....	.....	.....
	2018– 92	4273	31	13	.....	.....	.....	.....
	–119	4269	33	9	.....	.....	.....	.....
	2412– 1	4033	40	13	.....	.....	.....	.....
	Total, 5 progenies		139	44	.....	.....	.....	.....

TABLE 8 (*concluded*)

Group	Pedigree nos.		Number of F_3 plants					
	F_2	F_3	Purple Ia	Sun red IIa	Dilute purple, IIIa	Dilute sun red IVa	Brown V	Green
5 (*continued*)	2411–5 x 2412–1	4032	4	1	.....	.....	.....	.....
	2434–1 x –1	4019, 4020	8	8	.....	.....	.....	.....
	Total, 2 progenies		12	9	.....	.....	.....	.....
6	4006– 1	5014, 5015	126	.....	37	.....	.....	.....
	4065–14	5209	42	.....	12	.....	.....	.....
	Total, 2 progenies		168	.....	49	.....	.....	.....

TABLE 9. F_4 PROGENIES OF SELF-POLLINATED PURPLE PLANTS OF F_3 LOTS CONSISTING OF COLOR TYPES Ia, IIIa, V, AND VIb

Group	Pedigree nos.		Number of F_4 plants			
	F_3	F_4	Purple Ia	Dilute purple IIIa	Brown V	Green VIb
1	5010– 7	7020, 7021	51	15	12	8
	– 9	7022, 7023	53	19	22	6
	–11	7024, 7025	46	17	26	5
	5011– 4	7028, 7029	35	17	14	1
	Total, 4 progenies		185	68	74	20
2	4276–32	5181, A170	46	12	......	......
	5010– 2	7092	14	2	......	......
	5011– 6	7091, 6837	28	14	......	......
	Total, 3 progenies		88	28	......	......
3	5011–2	7026, 7027	67	......	21	......

TABLE 10. F_3 PROGENIES OF F_2 SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute sun red IVa	Green
					(VIa, c)
1	1513–152	2038, 2474, 4292	38	11	11
	2018– 4	4286	19	7	*16
	– 39	4287	30	12	11
	– 44	4288	9	4	6
	– 56	4289	30	8	11
	Total, 5 progenies		126	42	55
	1513–100 x 1516–20	2039, 4293	7	8	†23
	2018– 56 x 2043–11	4290	3	1	7
	2020–118 x –11	4291	4	9	20
	Total, 3 progenies		14	18	50
2	4037–2	5126, 5127	23	9	....
3	4037–24 x 2921–15	5128, 5129, 7074	50	....	(VIa) 43

* Plus one brown V plant.
† Plus one purple Ia plant.

TABLE 11. F_3 PROGENIES OF F_2 DILUTE PURPLE PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Dilute purple IIIa	Dilute sun red IVa	Green
					(VIb, c)
1	2018–18	4296	14	6	12
	4037– 9	5117, 5118	38	9	16
	5099– 7	A77	35	15	19
	A120– 13	A229	8	1	3
	Total, 4 progenies		95	31	50
	2922–16 x 4037–9	5119–5121	21	25	57
2	4066–9	5219	57	21	....
					(VIb)
3	4037–14	5122, 5123	16	....	5
	5095–29	A63	9	....	1
	5290–12	7056, 7057	60	....	14
	Total, 3 progenies		85	....	20
4	4065–50	5212	21	....	....

TABLE 12. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Dilute sun red IVa	Green VIc
1	4036–9	5115	16	6
	6750–4	7247, 7399	34	8
	A120–8	A228	12	3
	Total, 3 progenies		62	17
2	4036–8	5116	27	....
	4042–2	5166	65	....
	Total, 2 progenies		92	....
	2922–18 x 4042–2	5169–5171	69	....

TABLE 13. F_3 PROGENIES OF F_2 BROWN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree nos. F_2	Pedigree nos. F_3	Number of F_3 plants: Brown V	Number of F_3 plants: Green
1				(VIa, b, c)
	1513–12	2025, 4313	33	35
	2020– 8	4309	16	13
	–47	4305	23	*11
	–98	4307	16	8
	4065–12	5211	8	7
	Total, 5 progenies		96	74
2				(VIa, b)
	1513– 16	2030	21	6
	– 39	2026	23	10
	–143	2027	30	9
	–194	2023	32	9
	2018– 69	2539, 2540, 4299,4300	94	25
	– 96	2338, 4302	64	20
	2020– 57	4306	29	9
	4037– 6	5130, 7076	46	12
	6748B–37	7401	15	4
	Total, 9 progenies		354	104
	4037–6 x 2922–6	5131–5133	34	41

* Plus one sun red IIa plant.

TABLE 14. PROGENIES OF F_2 AND F_3 BROWN PLANTS, OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V, CROSSED WITH DILUTE SUN RED IVa PLANTS

Group	Pedigree nos.		Number of F_3 plants			
	F_2 x IVa	F_3	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2018–69 x 2192–18..	2386, 4301..........	30	35	......	....
	4370– 5 x 3000– 2..	4746, 4747..........	8	10	......	....
	Total, 2 progenies......................		38	45	......	....
2	2410–4 x 2417–2....	2993, 2994..........	9	......	6	....
	–6 x –1....	2995–2998..........	23	......	32	....
	Total, 2 progenies......................		32	......	38	....
3	5095–20 x L170–1 ..	S17................	15	......	......	....
	F_3 x IVa	F_4	Number of F_4 plants			
4	2025–10 x 2192–14..	4315...............	1	2	6	3
5	2030–13 x 2192–14..	4319...............	7	6	......	....
	2043– 2 x 2026–17..	2347, 4326..........	15	18	......	....
	Total, 2 progenies......................		22	24	......	....
6	2023–19 x 2192–12..	2332, 4311..........	19	......	26	....
	–23 x –12..	2330, 4310..........	15	......	16	....
	2027– 9 x –14..	2334, 4316..........	15	......	18	....
	5500– 5 x 5130– 1..	A65................	24	......	25	....
	Total, 4 progenies......................		73	......	85	....
7	2025–23 x 2192–14..	2333, 4314..........	25	......	......	....
	4253– 2 x 4299– 2..	5528, 6748A........	*46	......	......	....
	4305– 5 x 4042– 2..	5193, 5194..........	24	......	......	....
	Total, 3 progenies......................		95	......	......	....

* Plus one dilute sun red IVa plant.

TABLE 15. F_3 PROGENIES OF SELFED AND BACKCROSSED GREEN PLANTS OF THE CROSSES PURPLE Ia x GREEN VIc AND DILUTE SUN RED IVa x BROWN V

Group	Pedigree Nos. F_2	Pedigree Nos. F_3	Number of F_3 plants (Green)
1			(VI)
	1513 – 42	2033	22
	–106	2036	18
	–111	2032	13
	4036 – 6	5114	22
	4037 – 29	5124, 5125	42
	4066 – 4	5215	32
	5095 – 30	A62	8
	6748B– 11	7402	22
	Total, 8 progenies		179
2	1514– 9	2034	20
	–37	2035	19
	–47	2037	18
	6749– 1	7242	19
	– 4	7243	20
	Total, 5 progenies		96
3			(VIa)
	2019– 40	2364, 4356	*26
	– 63	2356, 4355	24
	– 92	2384	10
	– 98	2374	10
	–106	2357	15
	Total, 5 progenies		85
4			(VIb)
	2019–33	2349, 4354	29
	–57	2373, 4353	34
	–73	2379	10
	–84	2383	14
	Total, 4 progenies		87
5			(VIc)
	2019–17	2395	14
	–25	2348, 4357	29
	Total, 2 progenies		43

* Plus one brown V plant.

TABLE 16. F_1 PROGENIES OF CROSSES OF GREEN VIa, VIb, AND VIc WITH DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	2047–25 x 2192–14	2392	16	....	....
	2049–12 x –14	2393	20	....	....
	4300–14 x 4364– 1	5198	52	....	....
	4307– 9 x 4042– 2	5183, 5184	60	....	....
	Total, 4 progenies		148	....	....
2	2036–9 x 2192–14	4320	....	9	....
	4725–2 x 5095–30	A96, A97	....	67	....
	Total, 2 progenies		....	76	....
3	2025–12 x 2192–14	2335	....	....	24
4	2019– 29 x 1946– 4	2398, 2399	30	....	19
	– 40 x 2192–18	2365, 4340	5	....	5
	– 63 x –18	2358, 4349	11	....	10
	– 92 x 1945–10	2385	13	....	12
	– 98 x –10	2375	11	....	12
	–104 x 2012– 1	2363	13	....	12
	–106 x 2192–18	2359, 4351	27	....	15
	Total, 7 progenies		110	....	85
5	2019–33 x 2192–18	2352, 4342	....	5	4
	–51 x 1946– 4	2361, 4347	....	19	15
	–57 x 2192–18	2369, 2370, 4345	....	8	14
	–73 x 1945–11	2377, 2378	....	2	6
	–84 x –10	2382, 4352	....	22	26
	Total, 5 progenies		....	56	65
6	2019–17 x 1945–11	2396, 2397	....	....	43
	–19 x –11	2381	....	....	19
	–25 x –11	2351, 4344	....	....	44
	Total, 3 progenies		....	....	106

TABLE 17. F_2 and Backcross Progenies of Dilute Sun Red IVa x Green VIc

Group	Pedigree nos. F_1	Pedigree nos. F_2	Number of F_2 plants: Dilute sun red IVa	Number of F_2 plants: Green VIc
1	1983–34	4502, 4503	27	11
	2854– 7	4677–4679	199	73
	2866– 1	6471, 6472	43	15
	Total, 3 progenies		269	99
2	F_1 x VIc			
	2854–13 x 2887–69	6325, 6326	87	96
	–16 x –69	6319–6321	42	45
	2861– 1 x –41	4686–4688	93	100
	2866– 2 x 2888– 2	5748–5750, 6485–6487	90	74
	4707–82 x 4685– 1	6533–6535	45	43
	Total, 5 progenies		357	358

TABLE 18. F_1 Progenies of Intercrosses between Green Plants, VIa, VIb, and VIc

Group	Pedigree nos. P_1	Pedigree nos. F_1	Number of F_1 plants: Brown V	Number of F_1 plants: Green VI
1	2019–25 x 2019–106	2354	....	23
2	2019–25 x 2019–33	2350, 4343	....	22
3	2019– 40 x 2019– 63	2367	....	25
	– 98 x – 40	2376	....	25
	–104 x –106	2362	....	22
	Total, 3 progenies		....	72
4	2019–57 x 2019–51	2371, 4346	....	24
5	2019– 33 x 2019–63	2355	6	19
	– 40 x –33	2366, 4341	8	28
	– 57 x –98	2372, 4350	14	26
	– 73 x –40	2380	7	16
	–106 x –51	2360	5	16
	Total, 5 progenies		40	105

TABLE 19. F_2 PROGENIES OF CROSSES BETWEEN BROWN V AND GREEN VIc

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Brown V	Green VIa, b, c
1514–12	2029	19	16
–23	2031	22	13
–38	2028	25	16
2983– 7	5071, 5072	40	44
–11	5070	15	11
2986– 4	5078	21	8
– 9	5077	46	36
4035–35	5110	14	6
4068– 4	5225	53	23
–10	5227	24	20
–11	5226	38	30
Total, 11 progenies		317	223

TABLE 20. F_3 PROGENIES FROM F_2 BROWN PLANTS OF THE CROSS BROWN V x GREEN VIc

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Brown V	Green VI
1	2031–28	4323	19	....
	–32	2323	10	....
	Total, 2 progenies		29	....
2	2031–20	2324, 2541, 2542, 2948, 2949	82	34
	–29	2327, 2328	18	6
	Total, 2 progenies		100	40
3	2029–27	2320, 4321	17	20
	–34	2315, 4322	22	19
	Total, 2 progenies		39	39

TABLE 21. F_2 PROGENIES OF THE CROSSES SUN RED IIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIa

Group	Pedigree nos. F₁	Pedigree nos. F₂	Number of F_2 plants: Sun red IIa	Number of F_2 plants: Dilute sun red IVa	Number of F_2 plants: Green VIa, c
1	1514–32	2040, 4294	53	16	19
	–76	2041, 4295	40	14	23
	2083– 1	4336, 4337	24	10	11
	– 2	4338, 4339	26	4	11
	2981– 3	4992, 4993	91	42	45
	– 4	4994–4996	203	55	84
	4014– 1	5554–5557	83	33	33
	– 3	5559–5563	47	13	13
	4019– 2	5691, 5692	28	6	18
	– 4	5685, 5686	20	2	12
	4020– 1	5708	28	12	10
	4035– 3	5111–5113	49	21	24
	4040– 2	5148, 5149	14	5	13
	6661– 9	7379	35	16	21
	6662– 1	7381	44	9	29
	– 8	7380	42	10	17
	Total, 16 progenies		827	268	383
2	2398– 2	4426, 4427	28	9	12
	4029– 1	5097	31	18	21
	4776– 1	6951–6953	127	38	71
	4780– 9	6960, 6961	92	25	42
	–11	6954–6956	65	30	33
	Total, 5 progenies		343	120	179
3	1416– 1 x 1430– 1	1494, 2074	39	39	92
	2888–22 x 4019– 2	5694B, 5695A	16	14	22
	2922–18 x 4014– 3	5563–5565	30	26	68
	4014– 1 x 2922– 1	5558	3	3	10
	4019– 2 x 2888– 1	5697, 5698	15	14	22
	– 4 x – 1	5689, 5690	24	13	31
	4020– 1 x 2887–69	5709	7	14	22
	Total, 7 progenies		134	123	267
4	2921–15 x 4029– 1	5654–5656	28	37	80
	4774– 1 x 4710–45	6945, 6946	78	71	151
	4781– 2 x 4707–35	6967, 6968	54	76	132
	4782– 5 x –18	6972, 6973	103	88	195
	–13 x –15	6974–6978, 7667, 7668	80	101	191
	4789– 4 x –19	6989, 6990	50	43	108
	6661– 9 x 6690–17	7328, 7329	17	17	38
	6790– 5 x 6809–18	7293	32	32	67
	Total, 8 progenies		442	465	962

TABLE 22. F_2 PROGENIES OF THE CROSSES DILUTE PURPLE IIIa x GREEN VIc AND DILUTE SUN RED IVa x GREEN VIb

Group	Pedigree nos.		Number of F_2 plants		
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa	Green VIb, c
1	1514–61	2044, 2560, 2561	44	14	16
	2019–10	2425, 2931, 2932	19	3	6
	2072– 1	4333, 4334	38	12	10
	– 9	4335	22	13	7
	2956– 2	4899–4904	153	58	73
	4035–33	5107	50	16	24
	4068– 6	5222	46	18	26
	–17	5223	44	15	11
	Total, 8 progenies		416	149	173
2	2361– 1	4424, 4425	14	4	4
	4070– 6	5235, 5236	133	51	52
	–11	5237, 5238	62	21	19
	5269– 3	6696, 6697	30	11	15
	A96–14	A416, A417	15	6	4
	A97–29	A407, A408	30	9	13
	Total, 6 progenies		274	102	107
	6790–1 x 6809–8	7292	26	20	56

TABLE 23. F_2 PROGENIES OF THE CROSS SUN RED IIa x BROWN V

Pedigree nos.		Number of F_2 plants			
F_1	F_2	Purple Ia	Sun red IIa	Brown V	Green VIa
5192–1	A99	14	4	5	1
–2	7767	37	5	9	2
–3	7766, S23	69	20	23	7
Total, 3 progenies		120	29	37	10

TABLE 24. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Sun red IIa	Dilute sun red IVa
1	413– 1	1298	40	13
	617–11	1235	15	4
	1520– 9	2017	31	8
	2065– 1	4330	14	5
	– 2	2431, 4331	48	15
	2414– 2	2987–2992	36	9
	2975– 4	4983–4986, 7001, 7002	373	123
	4028– 3	5643–5646	22	7
	4040– 3	5150, 5151	41	8
	4332–26	5491–5493	55	16
	4787– 4	6779–6782	166	50
	5165– 2	A114	55	20
	7224– 4	8118, 8119	43	12
	7359– 1	8170, 8171	9	3
	7854– 1	8094, 8095	35	15
	A119– 4	A227	15	6
	Total, 16 progenies		998	314
2	F_1 x IVa			
	2065– 1 x 2043– 2	4329	27	30
	– 2 x – 2	2432, 4332	6	13
	4714–11 x 4774– 1	6943, 6944, 7676, 7677	173	133
	7224– 9 x 7225– 7	8115, 8116	196	180
	7354– 1 x 7315– 5	8250, 8251	86	96
	7770– 1 x 7768–172	8731	16	14
	– 5 x –172	8732	17	11
	A140–14 x A105– 6	A252, A468	92	87
	L1773–15 x L2049– 11	8741	46	37
	–20 x – 10	8742	41	39
	L1844–14 x L2048– 24	8743	37	41
	L2063– 5 x – 8	8746	56	48
	–26 x L2049– 3	8745	7	7
	L2064– 2 x L2048– 22	8744	11	6
	Total, 14 progenies		811	742

TABLE 25. F_3 PROGENIES OF F_2 SUN RED AND DILUTE SUN RED PLANTS OF THE CROSS SUN RED IIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Sun red IIa	Dilute sun red IVa
1	2990– 1	5776–5778	....	10
	4133–26	5366	....	40
	Total, 2 progenies		....	50
2	2991–1	5779, 5780	10	....
	–4	5781	9	....
	Total, 2 progenies		19	....
	7001–7 x 7002–11	7684, 7685	101	....
3	1235– 1	1633–1635, 2009	23	10
	1298–14	2011	14	2
	2987– 2	4997, 4998, 6999, 7000	324	111
	– 9	4999	12	4
	Total, 4 progenies		373	127

TABLE 26. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants	
	F_1	F_2	Dilute purple IIIa	Dilute sun red IVa
1	483– 3	884	16	5
	848– 2	1574	20	10
	2425– 2	2946, 2947	47	16
	4040– 1	5145–5147	69	26
	4070– 8	5240–5242	65	18
	–15	5234	27	8
	A119– 3	A226	17	4
	Total, 7 progenies		261	87
2	F_1 x IV			
	7317– 6 x 7322– 4	8204, 8205	18	22
	A106– 6 x A140–31	A249, A467	85	95
	A140–12 x A105– 3	A250, A251, A465, A466	83	51
	L1760– 6 x L2026–15	8739	56	63
	L1838–16 x –15	8738	33	32
	Total, 5 progenies		275	263

TABLE 27. F_1 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_1 plants		
	P_1	F_1	Purple Ia	Sun red IIa	Dilute purple IIIa
1	1529–18 x 1542–8......	2057...............	10	....	....
	6889– 1 x 6835–1......	7627...............	14	....	....
	Total, 2 progenies........................		24	....	....
2	2903–2 x 2947–37......	4796–4799..........	74	75	....
3	488– 9 x 730– 3.....	842, 1389...........	18	....	23
	1529–15 x 1549–35.....	2058...............	10	....	6
	Total, 2 progenies........................		28	....	29

TABLE 28. F_2 PROGENIES OF THE CROSS SUN RED IIa x DILUTE PURPLE IIIa

Pedigree nos.		Number of F_2 plants			
F_1 x IVa	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
6650– 9 x 6691– 8......	7337...........	8	12	13	6
6651–10 x – 8......	7338...........	7	7	5	6
7700– 4 x 7768–172......	8723, 8724......	9	8	6	5
–14 x –172......	8725, 8726......	13	10	12	15
7769– 2 x –172......	8729, 8730......	8	14	14	12
– 5 x 7315– 10......	8263, 8264......	19	22	18	15
– 7 x – 9......	8261, 8262......	35	37	36	24
Total, 7 progenies..................		99	110	104	83

TABLE 29. F_2 PROGENIES OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos. F_1	Pedigree nos. F_2	Number of F_2 plants: Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	478– 3	880	53	18	12	4
	– 4	881	49	20	11	5
	479– 1	883	43	15	12	3
	484–24	907, 1531	39	11	13	5
	–26	828, 1396, 1530	74	25	23	10
	739– 1	1312, 1549	97	27	28	8
	849– 1	1553, 1554	40	10	14	2
	850– 3	1559	10	5	0	1
	851– 2	1563	23	5	3	0
	– 3	1565	16	4	7	1
	852– 1	1566, 1567	14	5	3	1
	– 2	1568	2	0	1	1
	1564–15	4102	13	2	1	0
	2971– 3	4968–4976	65	22	23	8
	4028– 1	5647	17	5	5	0
	– 6	5082, A66	138	41	45	14
	4045– 3	5154	40	10	13	5
	4046– 4	5159, 5160	65	23	18	6
	4070– 4	5239	34	10	9	3
	–12	5232, 5233	7	1	2	2
	5165– 8	A117	40	14	13	5
	5172– 3	A126	17	7	6	1
	5179– 1	A130	42	15	11	7
	– 6	A131	12	1	4	3
	5180– 5	A133	36	11	10	3
	S12–18	A208	27	9	9	2
	Total, 26 progenies		1,013	316	296	100
2	F_1 x IVa					
	740– 2 x 732– 1	1118, 1119	39	33	36	35
	1105– 9 x 849– 3	1557, 1558	15	14	14	15
	–15 x – 1	1561, 1562	11	11	7	8
	–16 x 852– 2	1570, 1571	13	10	12	11
	1106–12 x 848– 1	1572, 1573	9	6	12	9
	1107– 4 x 851– 2	1564	4	6	8	4
	–13 x 850– 3	1560	10	7	12	8
	2922–19 x 4046– 4	5161, 5162, A142, A143	37	34	39	30
	4045– 3 x 2922–18	5155, 5156	23	17	13	17
	4046– 4 x 4042– 2	5164, 5165, A105–A107	26	23	27	26
	4729– 8 x 5165– 8	S12	7	2	5	5
	5812– 3 x 5179– 6	A132	6	9	3	5
	6785– 1 x 6784–18	7429, 7430	10	14	17	9
	– 1 x –26	7431, 7432	31	31	36	26
	7226– 2 x 7268– 2	8111	33	30	32	27
	7263– 9 x 7240–10	8008	14	15	18	14
	A140–18 x A106–4	A248, A469	35	44	34	40
	Total, 17 progenies		323	306	325	289

TABLE 30. F_3 AND F_4 PROGENIES OF F_2 AND EQUIVALENT F_3 PURPLE PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos. F₂	Pedigree nos. F₃	Number of F_3 plants: Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	271- 9	496, 497, 722	34	11	9	5
	1312-52	1535, 1577	35	13	9	1
	-59	1536, 2002	42	14	10	2
	4102- 2	5177	25	8	8	3
	5082-23	6742, A68	48	24	18	8
	-33	6743, A69	74	32	22	9
	5159- 3	A147	10	3	2	0
	Total, 7 progenies		268	105	78	28
	1312-59 x 1140-18	1575, 1576, 2000, 2001	26	25	24	21
2	271- 5	489, 490	12	5	......	......
	1312-87	1537	34	16	......	......
	5160- 8	A149	14	1	......	......
	Total, 3 progenies		60	22	......	......
	148- 1 x 271- 5	478, 479	12	6	......	......
	1312-87 x 1140-18	1578	9	13	......	......
	4102-13 x 4042- 2	5179, 5180, A113	11	12	......	......
	Total, 3 progenies		32	31	......	......
3	271- 3	492, 493	49	......	10	......
	1312-50	1534	44	......	18	......
	-81	1581	43	......	11	......
	4102-12	5178	26	......	9	......
	Total, 4 progenies		162	......	48	......
	271-12 x 80-8	483, 484	17	......	15	......
	F₃	**F₄**	**Number of F_4 plants**			
4	722- 5 x 720- 1	739, 762, 856, 1550	41	54	......	......
	A68-31	A339	13	5	......	......
5	722-3 x 719-3	740, 761, 849, 850	40	......	44	......
	-3 x 721-7	848	12	......	8	......
	Total, 2 progenies		52	......	52	......
6	722-1	760, 905, 1121, 1526	69	......	......	......
	724-1 x 722-1	857	18	......	......	

TABLE 31. F_3 PROGENIES OF SUN RED, DILUTE PURPLE, AND DILUTE SUN RED F_2 PLANTS OF THE CROSS PURPLE Ia x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants		
	F_2	F_3	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa
1	1312- 4	1579	17	....	....
	-36	1542	18	....	....
	-55	1543	18	....	....
	Total, 3 progenies		53	....	....
	1312-38	1580, 2010	24	....	7
	5159- 8	A148	14	....	5
	A132- 3	A233	16	....	7
	A133-12	A193	16	....	5
	Total, 4 progenies		70	....	24
2	80- 4	487, 488	....	30	....
	271- 4	494	....	50	....
	A117-12	A473	....	17	....
	Total, 3 progenies		....	97	....
	271- 1	491	....	55	25
	- 7	495	....	42	16
	1312- 3	1538	....	46	16
	-65	1539, 1999	....	36	12
	5234- 1	A86	....	11	5
	- 8	A87	....	27	12
	Total, 6 progenies		....	217	86
3	80- 8	485, 486	....	....	19
	1312-11	1544, 1872	....	....	27
	A133- 3	A192	....	....	26
	Total, 3 progenies		....	....	72

TABLE 32. F_2 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Pedigree nos.		Number of F_2 plants	
F_1	F_2	Weak sun red IIb	Dilute sun red IVa
2187–21	4135, 5371	151	41
–23	4133, 5365	160	59
2189–16	4138, 5377	112	25
2190– 4	5373	122	44
– 4 x 2187– 1	4142, 5374	99	42
– 7 x –23	4143, 5376	176	75
– 7	2391, 4144, 5375, 7072	141	49
4022– 5	5715	17	7
4134–22	5370	35	14
–56	5378	89	27
4162–41	5411	17	3
5364– 6	A58	181	43
Total, 12 progenies		1,300	429

TABLE 33. F_3 PROGENIES OF THE CROSS WEAK SUN RED IIb x DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_3 plants	
	F_2	F_3	Weak sun red IIb	Dilute sun red IVa
1	4136–43	5384, 6805, 7740	77	....
2	4136–11	5383, 6802	86	39
	4138–15	5385	22	8
	5365–26	A61	13	5
	5371–23	6798	7	2
	Total, 4 progenies		128	54
3	4143–23	5392, 5393	....	95

TABLE 34. F_2 PROGENIES OF THE CROSSES WEAK PURPLE Ib x DILUTE PURPLE IIIa, WEAK PURPLE Ib x DILUTE SUN RED IVa, AND WEAK SUN RED IIb x DILUTE PURPLE IIIa

Group	Pedigree nos.		Number of F_2 plants			
	F_1 x IIIa, IVa	F_2	Weak purple Ib	Weak sun red IIb	Dilute purple IIIa	Dilute sun red IVa
1	A208–15 x A445– 1..	A822..............	4	......	4	....
	A452– 4 x 7302– 4..	A789, A790.......	53	......	57	....
	–18 x –44..	A791, A792.......	84	......	102	....
	Total, 3 progenies..................		141	......	163	....
2	7507– 2 x A438– 5..	A793–A796.......	77	86	61	56
	A292–17 x A441– 6..	A788..............	55	58	49	38
	A441– 2 x 7515– 3..	A783..............	76	80	69	108
	– 6 x – 8..	A784..............	64	68	69	88
	– 7 x – 8..	A785..............	68	60	66	53
	–12 x A339–10..	A786..............	64	70	69	103
	–18 x 7515– 4..	A787..............	77	104	77	91
	Total, 7 progenies..................		481	526	460	537
3	S27–2 x 6805–9......	7773, 7774........	21	28	22	27

TABLE 35. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos.		Number of F_2 plants					
F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green IIIg, IVg, VI
2400– 1.........	2958–2961...	19	5	6	1	5	2
2952– 1.........	4844–4860...	59	21	8	1	14	18
–11.........	4861–4871...	43	15	7	4	11	15
–24.........	4872–4884...	42	12	9	2	15	16
–32.........	4885–4898...	62	23	12	3	20	17
2953–10.........	4822–4829...	84	24	25	8	23	30
Total, 6 progenies		309	100	67	19	88	98

TABLE 36. F_2 PROGENIES OF THE CROSS GREEN IVg x BROWN V

Pedigree nos. F_2	Number of F_2 plants									
	Purple			Sun red			Dilute purple	Dilute sun red	Brown	Green
	Purple anthers Ia	Green anthers Ig	? anthers I	Pink anthers IIa	Green anthers IIg	? anthers II	Purple anthers IIIa	Pink anthers IVa	Green anthers V	Green anthers IIIg, IVg, VI
2958–2961........	14	5	0	1	1	3	6	1	5	2
4822–4829........	61	12	11	10	4	10	25	8	23	30
4844–4860........	42	16	1	10	7	4	8	1	14	18
Total, 3 progenies.	117	33	12	21	12	17	39	10	42	50

TABLE 37. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN VIc

Group	Pedigree nos.		Number of F_2 plants					
	F_1	F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Brown V	Green
			(Ia, g)	(IIa, g)				(IIIg, IVg, VI)
1	5534–39..........	6795, 6796..	65	11	6	7	15	26
	6655– 6..........	7376.......	15	2	3	2	5	1
	Total, 2 progenies..............		80	13	9	9	20	27
	F_1 x VIc		(Ia)	(IIa)				(VI)
2	6655– 6 x 6690–17..	7349.......	6	13	13	15	17	46
	6808–13 x 6790– 8..	7290.......	30	16	18	16	14	49
	Total, 2 progenies..............		36	29	31	31	31	95
	F_1 x IVa							
3	6779–2 x 6790–8....	7299, 7300..	27	25	30	31	......	....
	6792–2 x –8....	7297.......	29	29	19	32	......	....
	–8 x –8....	7296.......	59	43	46	48	......	....
	Total, 3 progenies..............		115	97	95	111	......	....
	F_1 x IVg		(Ia, Ig)	(IIa, IIg)				(IIIg, IVg)
4	6656–9 x 6652–6....	7344.......	23	15	10	15	......	13

TABLE 38. F_2 PROGENIES OF THE CROSSES PURPLE Ig x DILUTE SUN RED IVa AND PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia, g	Sun red IIa, g	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2954–3..	5042–5045.	43	14	13	5	7
	2956–3..	4905–4914.	144	42	25	14	7
	–4..	4915–4929.	56	15	21	3	6
	Total, 3 progenies....		243	71	59	22	20
2	2421–1..	2910, 2911.	14	7	5	1	1
	–2..	2908, 2909.	26	13	4	1	0
	Total, 2 progenies....		40	20	9	2	1

TABLE 39. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
1	2909–16..........	5251, 5252	(Ia, g) 9	(IIa, g) 4	3	0	0
	F_2 x IVg 2909–4 x 2884–21	5255.....	15	15	5	1	(IIIg, IVg) 9
	F_2 x VIc 2909–4 x 2887–38	5256, A94.	(Ia) 27	(IIa) 19	15	14	....
2	5251–6...........	6708.....	31	7	......	......	....
3	2909–9...........	5257, 5258	(Ig) 14	(IIg) 2	......	......	5
	5252–1...........	6652.....	23	9	......	......	9
	Total, 2 progenies............		37	11	......	......	14

TABLE 39 (*concluded*)

Group	Pedigree nos.		Number of F_3 and F_4 plants				
	F_2 and F_3	F_3 and F_4	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green
3 (*continued*)	F_2, F_3 x IVg		(Ig)	(IIg)			(IIIg, IVg)
	2909– 9 x 2884–21	5259, 5260, 7007, 7008, 7060, 7061.	19	18	......	......	34
	4717–71 x 5252– 1	6654A.....	11	8	......	......	13
	5252– 1 x 5669– 3	6654B.....	4	6	......	......	6
	Total, 3 progenies.............		34	32	......	......	53
	F_2, F_3 x VIc		(Ia)	(IIa)			
	2909– 9 x 2887–38	5261, 5262.	14	11	7	11	....
	4057– 1 x 2909– 9	5534, 6790.	16	10	13	18	....
	5251– 1 x 5813–18	6655......	9	16	7	14	....
	5813–18 x 5251– 1	6656......	5	11	6	9	....
	Total, 4 progenies.............		44	48	33	52	....
4			(Ig)				(IIIg)
	2909–34..........	5253, 5254, 7090.....	26	......	......	......	6
	5251– 7..........	6658, 7015.	30	......	......	......	12
	Total, 2 progenies.............		56	......	......	......	18
	F_3 x IVg 4717–20 x 5251–7..	6659, 7014.	28	......	......	......	27

TABLE 40. F_3 AND EQUIVALENT F_4 PROGENIES FROM F_2 AND F_3 SUN REDS AND DILUTE PURPLES OF THE CROSS PURPLE Ia x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Sun red	Dilute purple IIIa	Dilute sun red IVa
1			(IIa)		
	2090–20	5278	30	....	8
	5251– 8	6648	37	....	10
	–10	6709	30	....	8
	Total, 3 progenies		97	....	26
2			(IIa, g)		
	2909– 8	5270–5273	43	....	....
	–26	5280–5283	64	....	....
	–32	5274–5277	121	....	....
	Total, 3 progenies		228	....	....
	F_2 x IVg				
	2909–26 x 2884–35	5284–5287, 7137	41	....	....
	F_2 x VIc		(IIa)		
	2909–26 x 2887–38	5288, 5289	67	....	....
	Total, 2 progenies		108	....	....
3	2909–21	5265, 5266	....	46	9
	F_2 x IVg				
	2909–21 x 2884–35	5267, 5268	....	44	31
	F_2 x VIc				
	2887–31 x 2909–21	5269	....	41	51
	Total, 2 progenies		....	85	82

TABLE 41. F_2 PROGENIES OF THE CROSS PURPLE Ig x GREEN IVg

Group	Pedigree nos. F_1	Pedigree nos. F_2	Purple	Sun red	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
			(Ig)	(IIg)			
1	5255 – 6	7094, 7095, 7701, 7702	80	24	......	......	55
	5259 – 3	7010, 7011	54	22	......	......	25
	6654B– 3	7375	23	7	......	......	9
	6659 –15	7365	28	12	......	......	12
	–22	7366	11	3	......	......	5
	–27	7368, 8491	43	17	......	......	24
	6660 – 9	7378	21	7	......	......	10
	–12	7377	33	13	......	......	10
	Total, 8 progenies		293	105	......	......	150
2	F_1 x IVa		(Ia)	(IIa)			
	6659–19 x 6691–8	7339	14	9	14	12	....
	6660– 3 x –8	7340	9	11	12	11	....
	F_1 x VIc						
	6654A–2 x 6690–9	7335	20	15	13	10	....
	B–1 x –17	7336	15	26	23	37	....
	Total, 4 progenies		58	61	62	70	....

TABLE 42. F_2 PROGENIES OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos. F_1	Pedigree nos. F_2	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg
1	2403–1	2962–2966	23	8	10
2	2420– 1	2904, 2905	17	5	9
	2954– 4	5038–5041	63	26	34
	2967– 2	6826, 6827	36	8	17
	–11	6828, 6829	78	32	31
	5263– 4	6669, 6670	31	16	8
	5267– 5	6675–6678	41	14	27
	–12	6679–6682	62	12	22
	Total, 7 progenies		328	113	148
3	F_1 x IVg 7322–3 x 7317–4	8210–8213	46	45	86

TABLE 43. F_3 AND F_4 PROGENIES FROM F_2 AND EQUIVALENT F_3 DILUTE PURPLES, DILUTE SUN REDS, AND GREENS, OF THE CROSS DILUTE PURPLE IIIa x GREEN IVg

Group	Pedigree nos.		Number of F_3 and F_4 plants		
	F_2 and F_3	F_3 and F_4	Dilute purple IIIa	Dilute sun red IVa	Green
1A					(IIIg, IVg)
	2966– 7	5049–5055	50	25	26
	5049–25	6816–6818, 7441	52	13	20
	5050– 6	6822–6824, 7058, 7059	41	10	27
	Total, 3 progenies		143	48	73
1B	6676–12	7383	26	10	16
	6828–12	7658–7660	14	4	7
	Total, 2 progenies		40	14	23
2	5052–7	6825, 7323, 7442	27	9	....
	6676–8	7382, A266	55	14	....
	Total, 2 progenies		82	23	....
3					(IIIg)
	5049–37	6819–6821	62	....	16
4					(IVg)
	2905–22	2547–2550	....	21	9
	5053– 1	6875, 6911, 6912	....	42	13
	Total, 2 progenies		....	63	22
5	5050– 1	6874	....	17	....
	5054–10	6745, 6872, 6873	....	108	....
	5055– 2	6871, 7315	....	51	....
	– 5	7515	....	21	....
	Total, 4 progenies		....	197	....
6					(IIIg, IVg)
	2905– 5	5243, 5244	....	....	5
	–19	5245, 5246	....	....	13
	5049–13	6913, 6914	....	....	11
	5052– 3	6833	....	....	24
	– 5	S5	....	....	15
	–12	6832	....	....	32
	6829– 9	7655–7657	....	....	30
	Total, 7 progenies		....	....	130

TABLE 44. F_2 PROGENIES OF THE CROSSES SUN RED IIg x GREEN IVg, SUN RED IIa x GREEN IVg, AND DILUTE SUN RED IVa x GREEN IVg

Group	Pedigree nos.		Number of F_2 plants			
	F_1	F_2	Sun red		Dilute sun red	Green
			Pink anthers IIa	Green anthers IIg	Pink anthers IVa	Green anthers IVg
1	4787–6	6983, 6984	......	122	....	52
	5284–3	7003–7006	......	94	....	25
	Total, 2 progenies		......	216	....	77
2	F_1 x IVg					
	7317–6 x 7318–4	8214–8217	22	31	24	32
	7318–1 x 7317–4	8222–8225	38	25	34	26
	–4 x –6	8218–8221	45	34	47	51
	Total, 3 progenies		105	90	105	109
3	5267–3	6671–6674	......	......	55	22
	F_1 x IVg					
	7031–14 x 6857–5	7725, 7726	......	......	30	30

TABLE 45. F_1 PROGENIES OF CROSSES OF SUN RED IIa AND DILUTE SUN RED IVa WITH GREEN IIIg AND IVg

Group	Pedigree nos.		Number of F_1 plants			
	P_1	F_1	Purple Ia	Dilute purple IIIa	Dilute sun red IVa	Green
1	IIa x IIIg					
	7097–5 x A159–25...	7710...........	33	......	....	....
	7357–3 x 7356– 1...	8151, 8152......	31	......	....	....
	Total, 2 progenies....................		64	......	....	....
	IVa x IIIg					
	A9–22 x 7097–1.....	7709..........	......	4	....	....
2	IVa x IVg					
	6860– 8 x 6869–1....	7713...........	......	......	28	....
	A9–14 x 7060–1....	7708, A283, A284	......	......	31	....
	Total, 2 progenies....................		......	......	59	....
	IVa x IIIg					
	6860–13 x 6871–39...	7714...........	......	11	12	....
	6861– 2 x 6751– 3...	7711...........	......	9	18	....
	Total, 2 progenies....................		......	20	30	....
	IVa x IIIg					(IIIg, IVg)
	6861–4 x 6882–5.....	7512, 7513, 7716.	......	25	11	34
	7039–3 x 7061–1.....	7727, 7728......	......	44	43	72
	Total, 2 progenies....................		......	69	54	106
3	IVa x IIIg					(IIIg)
	7312–8 x 7313–2.....	8183...........	......	86	....	92
	7313–2 x 7314–1.....	8184...........	......	31	....	19
	7314–1 x 7313–1.....	8200, 8201.....	......	126	....	129
	–6 x –2.....	8185...........	......	85	....	98
	Total, 4 progenies....................		......	328	....	338

TABLE 46. F_2 PROGENIES OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos. F_1	Pedigree nos. F_2	Number of F_2 plants: Dilute sun red IVa	Number of F_2 plants: Green
				(IVg, VIc)
1	5534–4	6791, 6792	35	29
	6530–1	7179, 7180	51	43
	–2	7181, 7182	32	30
	6531–1	7177, 7178	64	42
	–2	7175, 7176	63	38
	7032–1	7163, 7164	52	39
	7036–3	7169, 7170	60	36
	7037–2	7171, 7172	63	34
	Total, 8 progenies		420	291
2	F_1 x VIc			(VIc)
	7032–7 x 6878–42	7729, 7730	24	24
	7034–5 x –42	7767, 7768	42	34
	Total, 2 progenies		66	58
	F_1 x IVg			(IVg)
	7037–4 x 7049–7	7173, 7174	48	50
	7049–1 x 7037–4	7731, 7732	48	46
	Total, 2 progenies		96	96

TABLE 47. F_3 PROGENIES OF F_2 DILUTE SUN RED PLANTS OF THE CROSS GREEN IVg x GREEN VIc

Group	Pedigree nos. F_2	Pedigree nos. F_3	Number of F_3 plants: Dilute sun red IVa	Number of F_3 plants: Green IVg, VIc
1	6791– 3	7148, 7149	23	19
	6792– 6	7154, 7155	69	45
	–11	7159	16	13
	Total, 3 progenies		108	77
2	6791–22	7150, 7151	65	23
	–23	7152, 7153	49	18
	6792– 7	7157	38	12
	–10	7158	23	10
	–13	7160	12	3
	Total, 5 progenies		187	66
3	6792– 5	7156	48	....
	–25	7161	30	....
	Total, 2 progenies		78	....

TABLE 48. F_2 AND F_3 PROGENIES OF THE CROSS GREEN IVg x GREEN VIa

Group	Pedigree nos.		Number of F_2 and F_3 plants		
	F_1	F_2	Sun red	Dilute sun red IVa	Green
1			(IIa, g)		(IVg, VIa, c)
	2400– 2	2902, 2903	7	3	5
	2952– 5	4838–4843	36	3	18
	–22	4830–4837	99	15	57
	2953– 4	4810–4813	88	32	59
	– 7	4814–4817	111	20	62
	–21	4818–4821	92	30	45
	2957– 2	4930, 4931	153	58	102
	Total, 7 progenies		586	161	348
2	F_2	F_3			
	4930–31	6991, 6992	119	....	....
3			(IIa)		(VIa)
	2903– 2	4783–4786	99	....	32
	4930–22	6993, 6994	130	....	39
	Total, 2 progenies		229	....	71
	F_2 x IVa				
	2903–2 x 2889–38	4787–4790	55	....	....

TABLE 49. F_2 PROGENIES OF THE CROSS GREEN IIIg x GREEN VIc, AND F_1 PROGENIES OF CROSSES OF F_2 GREENS WITH SUN RED IIa AND DILUTE SUN RED IVa

Group	Pedigree nos.		Number of F_2 plants				
	F_1	F_2	Purple Ia	Sun red IIa	Dilute purple IIIa	Dilute sun red IVa	Green IIIg, IVg, VIb, c
1	2907-8	5297, 5298	.....	.....	28	11	38
	5262-5	7085, 7086, 7722, 7723	.....	.....	81	26	97
	Total, 2 progenies		.....	.....	109	37	135
	P_1	F_1	Number of F_1 plants				
2	IIIg x IIa 7085-10 x A159-24	7717	27	.....	.....	.....	.....
	IIIg x IVa 7086-2 x 7102-7	7207	.....	.....	14	.....	.....
	-3 x -8	7719	.....	.....	25	.....	.....
	Total, 2 progenies		.....	.....	39	.....	.....
3	IIIg x IIa 7086-6 x A159-17	7718, A298, A299	28	41	.....	.....	.....
	IIIg x IVa 7086-4 x 7102-8	7720	.....	.....	11	9	.....
4	IVg x IVa 7086-8 x 7102-8	7721	.....	.....	.....	22	.....

ANTHER, GLUME, AND RACHIS COLOR OF PURPLE

1, Purple, type Ia, typical, anthers purple; 2, type Ia with r^{ch}, anthers near-black; 3, type Ia with *pr*, anthers reddish; 4, type Ig, with R^g or r^g, anthers green

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF DILUTE PURPLE AND GREEN

1, Dilute purple, type IIIa, typical, anthers purple; 2, type IIIa with r^{ch}, anthers near-black; 3, type IIIa with *pr*, anthers reddish
4, Green, types IIIg and IVg with R^g or r^g, green thruout

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF SUN RED AND DILUTE SUN RED

1. Sun red, type IIa, intensely pigmented form

2. Dilute sun red, type IVa, intensely pigmented form: 3 and 4, near-green forms, little color in glumes, anthers green with reddish stippling as shown in enlarged anther

(Drawings by C. W. Redwood, somewhat diagrammatic)

ANTHER, GLUME, AND RACHIS COLOR OF BROWN AND GREEN

1, Brown, type V, intensely pigmented, homozygous form; 2, type V, less intensely pigmented form, heterozygous for *B* or *Pl* or both

3, Green, type VIc; 4, type VIb, green with tinge of brown due to *Pl* and r^{ch}

(Drawings by C. W. Redwood, somewhat diagrammatic)

CULM, HUSK, AND SHEATH COLOR OF PURPLE AND SUN RED

1, Purple, type Ia; 2, weak purple, type Ib

3, Sun red, type IIa; 4, weak sun red, type IIb; 5, type IIb, inner husks of lower ear highly colored from exposure to sunlight directly after being torn apart

(Drawings 1 and 3 by C. W. Redwood; 2, 4, and 5 by Bernice M. Branson)

CULM, HUSK, AND SHEATH COLOR OF DILUTE PURPLE, DILUTE SUN RED, BROWN, AND GREEN

1, Dilute purple and dilute sun red, types IIIa and IVa; 2, more highly colored form of types IIIa and IVa

3, Brown, type V

4, Green, types VIb and VIc; 5, type VIa, with some brown in outer husks due to *B*

(Drawings by C. W. Redwood)

MATURE CULM, HUSK, AND COB COLOR

1, Purple, type Ia; 2, sun red, type IIa; 3, dilute purple, type IIIa; 4, more intensely pigmented form of type IIIa; 5, brown, type V; 6, dilute sun red, type IVa

(Drawings by Carrie M. Preston)

DEVELOPMENT OF COLOR IN DARKNESS

Tassels and sheaths developed under black paper bags: 1, purple, type Ia; 2, brown, type V; 3, dilute purple, type IIIa; 4, sun red, type IIa, no red color

(Drawings by Carrie M. Preston)

RELATION OF SOIL FERTILITY TO COLOR DEVELOPMENT

Young plants of dilute sun red, type IVa: 1, plant grown in fertile soil; 2, plant grown in infertile soil

(Drawing 1 by Bernice M. Branson; 2 by Carrie M. Preston)

COLOR DEVELOPMENT IN BROKEN LEAVES

1. Dilute sun red, type IVa, about one week after the leaf was creased; 2, dilute purple, type IIIa with japonica white stripes, about three days after the leaf was creased

(Drawings by Carrie M. Preston)

ABERRANT COLORATION OF BROWN TASSEL

Poorly developed tassels of brown, type V, sometimes exhibit purple in abnormally developed parts

(Drawing by Carrie M. Preston)

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

SOME EFFECTS OF POTASSIUM SALTS ON SOILS

R. S. SMITH

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CONTENTS

SOME EFFECTS OF POTASSIUM SALTS ON SOILS

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R. S. Smith

The factors that determine the ability of a soil to support plant growth are known to be very complex, and any modification of this ability brought about by materials added to the soil is at least equally complex. It is now generally recognized that the secondary effects of fertilizing materials which are added to a soil may ultimately prove either beneficial or injurious when measured in terms of crop yields. The deleterious effects of ammonium sulfate have been particularly noted. The secondary effects of other fertilizer salts have been less thoroly studied because their action is thought to be less pronounced. However, attention has been called to various effects exerted by other materials, including the salts of potassium. The somewhat conflicting experimental data bearing on the effects of the chloride and the sulfate of potassium on the soil as a medium for plant growth led to the work reported in this paper.

The method of attacking the problem was, first, to determine the effect of various applications of potassium chloride and potassium sulfate on the growth of wheat, both in the variously treated soils and in water extracts of the soils; and secondly, to attempt to get at the causes of the effect of these salts on crop growth as noted in this work and as noted by other investigators.

HISTORICAL REVIEW

EFFECT OF POTASSIUM AND MANGANESE SALTS ON PLANT GROWTH

Potassium salts

The stimulative action on the growth of the higher plants exerted by the salts of potassium which are commonly used as fertilizing materials, is recognized. That this action is in part secondary seems evident from the fact that the specific effects noted vary with different soils and with the same soil variously treated.

Ordinarily, these salts would probably not be used in sufficient quantity to prove directly harmful to plant growth; but under certain intensive systems of farming, in which heavy applications of fertilizers are made,

such a result might follow. Lyon, Fippin, and Buckman (1915) make the statement that "it [potassium] may be present in large quantities in the soil and yet exert no harmful effect on the crop." Whether this statement refers to soluble salts of potassium added to the soil, or to the slowly soluble compounds in the soil minerals, is not stated. There is a possibility, however, that even the ordinary applications of potassium salts may result in an increased loss from the soil of other bases, particularly calcium.

But little work has been done to determine at what concentration the salts of potassium become toxic to plant growth in soils. Headden (1915) found that yellow-berry in wheat is increased by the application of 150 pounds of potassium to the acre. He ascribes this condition to the excess of soluble potassium over soluble nitrogen. This effect of a comparatively small application of a potassium salt in aggravating an abnormal condition in the wheat crop is of interest in this connection in that it indicates a significant modification of the soil as a medium for plant growth.

Harris (1915), from an extensive investigation of the effect of alkali salts on the germination and growth of seedlings in three different soils, reports the concentrations of potassium chloride and potassium sulfate at which these salts become harmful to wheat seedlings. He found that heavier applications of these salts were required to cause injury to the seedlings than would ever be applied, even in the most intensive systems of farming.

McCool (1913) determined the effect of the chlorides of ammonium, magnesium, potassium, and calcium on the germination of pea seeds in soil. The salts were harmful in the order given. Potassium chloride caused slight injury when used at the rate of about 7456 pounds in 2,000,000 pounds of soil. The character of the soil is not stated by the writer.

Voelcker (1909), in conducting pot experiments with wheat at the Woburn experiment station, in which the chloride, the sulfate, the carbonate, and the nitrate of potassium were used in such amounts as to supply the soil in each case with 0.0075 per cent of the metal potassium — which is equivalent to 166 pounds of the chloride, 312 pounds of the sulfate, 248 pounds of the carbonate, and 369 pounds of the nitrate, per 2,000,000 pounds of soil — noted injury with the carbonate. It is difficult

to understand how such small applications of any of these salts could cause injury to wheat.

Much work has been done on the toxicity of bases in solution cultures with various crop plants. This phase of the study is typified by the investigations of McCool (1913) on a large number of bases, including potassium. This type of investigation, however, has little direct significance in soil studies, because the conclusions drawn cannot be applied with a soil medium due to side reactions which are involved when so complex a medium is employed. McCool found that the chlorides of barium, manganese, ammonium, magnesium, sodium, potassium, and calcium were toxic to pea seedlings in the order named. It is of interest to note that manganese stands near the head of the list.

The degree of toxicity of all the salts is much less in soil than in nutrient solution. As has been noted, McCool found that potassium chloride caused slight injury to the germination of pea seeds in soil when applied at the rate of about 7456 pounds to 2,000,000 pounds of soil, and Harris reports much higher concentrations than this as being necessary to produce a toxic condition except in the case of coarse sand.

It thus appears that injury to plant growth has been found to result from the use of potassium salts in large quantities; that applications at the ordinary rate have been found to cause injury in but one case; and that small applications may possibly accentuate pathological conditions in the growing plant.

No reports of experiments on the growth of seedlings in soil extract made from soils to which only potash salts had been added, have been found in the literature.

Abbott, Conner, and Smalley (1913) report some soil-extract-culture experiments with corn, using soil high in soluble aluminium salts. This work is of interest in this connection in that it agrees with the conclusions of other investigators that the water extract from unproductive field soils is toxic to the root growth of seedlings.

Manganese salts

Manganese, as is noted later in this paper, is one of the bases replaced by potassium in some soils, and, since it has been shown by some investigators to have considerable influence on plant growth, a brief review of the literature regarding its action is here given.

As shown by Skinner and Sullivan (1914), manganese increases the oxidizing power of plant roots. This, however, was not accompanied by increased growth when the plants were grown in fertile soil. Infertile soils seemed to respond to manganese when it was used in small quantities, varying from 5 to 50 parts of manganese to 1,000,000 parts of soil.

Experiments by Skinner and Reid (1916) on silty clay loam of an acid nature at Arlington, Virginia, in which manganese sulfate was applied annually at the rate of 50 pounds to the acre previous to planting, show a decrease in the yield of wheat and cowpeas and inconsistent results with rye. When the lime requirement of the soil was just satisfied, the depression was decreased; and when an excess of lime was used, the crop yields were increased by manganese, except in the case of potatoes.

The results of other workers agree in the main in showing that the salts of manganese increase the yields of field crops when used in small quantities. In some instances a decrease results, and the work of Skinner and Reid seems to indicate that the reaction of the soil is an important factor.

Little work has been done to determine at what concentrations salts of manganese become toxic to plant growth in soils. McCool (1913), using a sandy loam soil, found that manganese chloride in solution was toxic to peas when added at the rate of 330 cubic centimeters of N/50 solution to 1000 grams of soil. This rate of application is equivalent to about 181 parts of the element manganese to 1,000,000 parts of soil. McCool found also that calcium overcame this injurious action, while Kelley (1908) reports that lime had no such effect.

The conclusion seems justified that if a neutral salt when added to the soil replaces even small amounts of manganese, the presence of this replaced base may affect crop growth adversely or occasionally beneficially, depending on other factors not well understood.

Other bases replaced by various fertilizer treatments are known to be toxic to plant growth, particularly iron and aluminium. But since neither of these elements was found to be present in the water extracts of the soils used in this work, no discussion of their action seems necessary.

EFFECT OF POTASSIUM AND MANGANESE SALTS ON NITRIFICATION IN SOILS

Potassium salts

Potassium salts have been found to produce specific effects on nitrification. Under certain conditions a stimulation has been noted, while under

other conditions the reverse has been the case. The literature has been searched in an attempt to discover what effects potassium salts have on nitrification, and any specific effects that have been found to accompany certain conditions resulting from the application of potassium salts to soils. A close correlation between the nitrifying power of a soil and its crop-producing power may not exist, but the two are likely to be associated. A study of the nitrifying power of a soil should, then, furnish some indication of its crop-producing power and help to explain any departures from the normal in crop growth.

Dumont and Crochetelle (1893) report favorable effects of potassium salts on nitrification in soils rich in organic matter and limestone. They later (1894) report work with a sandy humous soil stated to be poor in lime. This soil as reported contained 17.5 per cent of humus and 0.285 per cent of limestone. Potassium carbonate and potassium sulfate, both with and without lime, were used in different amounts. Potassium carbonate was used in increasing amounts from 0.1 to 6 grams, to 100 grams of soil. Marked stimulation was found to accompany its use up to 4.5 grams, and then there was a steady decrease in the nitric nitrogen found. Potassium sulfate without lime had no consistent effect. The character of the results indicates that the differences found in the latter treatments were due to factors other than those under study. When 2.5 grams of limestone were applied in addition to the potassium sulfate, there was a constant increase in the amount of nitric nitrogen found with an increase in the amount of potassium sulfate used, the heaviest application being 5 grams to 100 grams of soil.

Lyon and Bizzell (1918) report the nitrogen recovered from the lysimeter tanks at Cornell University. Apparently potassium sulfate without lime depressed nitrification. Lime counteracted this effect, but even with lime the sulfate did not cause any appreciable stimulation of the process.

Greaves (1916), in laboratory experiments on the effect of potassium salts on the bacterial activities of sedimentary soils derived from limestone and quartzite, found that potassium chloride and potassium sulfate used at the rate of from 6.1 to 8602 parts per million depressed nitrification at all concentrations. Potassium nitrate and potassium carbonate, used at the same rates, stimulated nitrification at the lower concentrations but became toxic at the higher, the nitrate at 48.9 parts per million and

the carbonate at 3910 parts per million. Greaves concluded that the extent of stimulation is governed largely by the cation, and that the toxicity of potassium salts is governed by the electro-negative ion combined with the potassium, since he found that the chlorides of sodium, magnesium, manganese, and iron, and the sulfates of calcium and manganese, increased bacterial activity, while the chlorides of potassium and calcium and the sulfates of sodium and potassium failed to cause any stimulation.

Pichard (1884) found that potassium sulfate caused strong nitrification of the organic nitrogen in a soil high in organic matter, but that its influence was not so marked as was that of calcium sulfate or sodium sulfate.

Allen and Bonazzi (1915) studied nitrification in soil samples from the plots at the Ohio experiment station. Ammonium sulfate in solution was used as the nitrifiable material at the rate of 21.2 milligrams of nitrogen per 100 grams of soil. The samples were incubated for ten days. The results with the samples from the potassium sulfate plots — which had received 80 pounds of the salt to the acre on corn, oats, and wheat of the five-years rotation — failed to show any increase in nitrification over the check; in fact, denitrification apparently took place in some cases.

Peck (1911) found that potassium sulfate used at the rate of 0.5 gram in 500 grams of sugar-cane soil decreased the bacterial activity, as measured by bacterial numbers and nitrogen fixation during one month of incubation.

Renault (1910) cites experiments by Dumont which show that slow ammonification and subsequent nitrification is always accompanied by a low percentage of potash.

It thus appears that potassium fertilizers, when applied at the usual rate under field conditions, commonly exert a depressing influence on nitrification. Under laboratory conditions both the chloride and the sulfate of potassium have generally been found to exert a depressing effect on nitrification, even when used in amounts as small as 12 pounds to 2,000,000 pounds of soil. Lime apparently counteracts the injurious effects of small applications of the sulfate and permits some stimulation of the process of nitrification.

Manganese salts

Salts of manganese are known to have marked influence on nitrification, and since manganese, as has already been stated, is one of the soil bases

replaced by potassium, it is of importance in this connection to note what its effects have been found to be.

Kelley (1912), working with Hawaiian soils, found that those high in manganese had a stronger nitrifying power than those low in this element. However, the soils high in manganese were in a better physical condition, and their higher nitrifying power was attributed to this fact rather than to any difference in manganese content.

Montanari (1914) found that manganese dioxide and manganese carbonate apparently stimulated nitrification, while the sulfate exerted less stimulation or even depressed the process.

Leoncini (1914) found that manganese dioxide increased nitrification when used in amounts as high as 2.2 per cent, but that heavier applications apparently had no influence.

Brown and Minges (1916) determined the effect of various manganese compounds on nitrification and ammonification in Carrington clay loam. In the ammonification tests dried blood was used, and in the nitrification trials ammonium sulfate was used. Manganese chloride apparently had no effect on nitrification in amounts less than 0.5 per cent; but from that point on, increasingly heavy applications caused increased depression, until, with 5 per cent of the salt, nitrification was inhibited. With manganese sulfate there was decisive depression of nitrification when 0.5 per cent of the salt was used, but with increasingly heavy applications the results did not show an increasing depression. Manganese nitrate apparently depressed nitrification, the magnitude of depression increasing with the amount of the salt used. Manganous oxide in most cases depressed nitrification, altho definite conclusions regarding this point cannot be drawn from the data presented.

Greaves (1916) found the chloride, the sulfate, and the nitrate of manganese toxic to ammonification in soil at concentrations of 68.6, 137.3, and 274.6 parts of added manganese, respectively, to 1,000,000 parts of soil. The carbonate of manganese was without effect even at the highest concentration used, 6045.6 parts per million.

Olaru (1915) reports three experiments on nitrogen fixation in nutrient solutions with varying amounts of manganese. He found that stimulation of the process resulted from all the concentrations of manganese used, but that the proportion of 1 part of manganese to 200,000 parts of solution gave the greatest stimulation. Olaru suggests that increases in

crop yields which have been found to follow the use of fertilizing materials are due, not only to the direct action of the materials on the plants, but also to their modification of the bacterial activities of the soil.

There appears to be much conflict in the data cited regarding the effect of manganese compounds on nitrification. In some cases very low concentrations of the various salts proved to be toxic, while in others relatively high concentrations were stimulative. Too little information is given regarding the nature of the soil used in the various experiments to permit any attempt to account for the discrepancies.

EFFECT OF REACTION OF THE SOIL ON NITRIFICATION

The reaction of the soil is generally considered to be an important factor in determining its capacity to support a vigorous nitrifying flora. Brown (1911:55) apparently takes an extreme position when he says: "The effect of lime on nitrification and the necessity for the presence of lime in the soil for the process to occur, have long been a matter of common knowledge."

The literature bearing on this problem is voluminous and no attempt is made here to summarize it. The stimulating action of lime on nitrification is generally conceded, but apparently the process may go on in soils very deficient in lime.

Fred and Graul (1916) state that "it seems that under laboratory conditions, the beneficial effect of calcium carbonate on plant growth must be accounted for by some processes other than the direct effect on nitrification." Temple (1914) and White (1914) report vigorous nitrification in strongly acid soils.

In the work herein reported, the heaviest treatments with the chloride and the sulfate of potassium caused a slight increase in the lime requirement of the soils, but in no case was the increase more than 300 pounds of calcium carbonate to 2,000,000 pounds of soil. This small difference in reaction is not considered significant so far as nitrification is concerned, particularly in view of the fact that nitrification has been shown to proceed in strongly acid soils. The increasing depression in nitrification which will be shown to have accompanied increasingly heavy applications of the potassium salts must be accounted for on some basis other than increased acidity.

INTERCHANGE OF BASES

As stated by Sullivan (1907), the fact that water is purified by filtration thru sand was known in the time of Aristotle. That common salt can be removed from water by filtering the water thru sand or soil has likewise been known for many years. Hilgard (1911 : 267) states that the latter is a clearly physical effect. When neutral salt solutions are filtered thru soil, the filtrate may be either acid or alkaline, depending on whether the cation or the anion of the salt has been removed the more strongly. This phenomenon has been attributed to selective ion adsorption. Truog (1916) and Sullivan (1907) think that it is better accounted for by an exchange of bases, in which the base of the soluble salt interchanges in part with the iron or the aluminium of the soil. The salts of the latter metals hydrolyze strongly in dilute solution and give an acid value.

The fact that soils enter into a chemical exchange with salt solutions was recognized at an early date by Thompson (1850), who found that an ammonium sulfate solution filtered thru soil gave up its ammonium in exchange for calcium. Way (1850, 1852, 1854), in a number of experiments, extended the observations of Thompson and found that the nitrates, the chlorides, and the sulfates of ammonium, potassium, sodium, and magnesium, when filtered thru soil, exchanged their bases for calcium from the soil. Way concluded that the active constituent of the soil entering into this interchange was a hydrated alumino-silicate of the clay fraction. It is now thought that any silicate is capable of entering into these reactions, according to Sullivan (1907).

Peters (1860) found that the absorption of the cation of a salt in neutral solution was of about the same magnitude regardless of the form of combination. Thus, he found that potassium was absorbed in about equal amount from equivalent solutions of its chloride, its sulfate, and its carbonate. In an extensive investigation Küllenberg (1867) confirmed Peters' conclusion. He found that the base entered into the reaction in about the same amount, whether it was combined with the sulfate, the nitrate, or the chloride.

The bases are mutually replacable, but are not replaced with equal facility. The stability of the silicate or the alumino-silicate is the controlling factor. Lemberg (1870, a and b, 1872, 1876), in a series of studies, found that the sodium in silicates is replaced more readily by potassium

than is potassium by sodium, and that magnesium is replaced less readily from its silicate by calcium than is calcium by magnesium.

Van Bemmelen (1878) treated a soil with a solution of potassium chloride, and found that the potassium had been exchanged for sodium, calcium, and magnesium. Van Bemmelen states that the absorption of the entire salt takes place very slightly if at all.

The important point brought out by Van Bemmelen in this early work and reemphasized by him later (Van Bemmelen, 1900), is that colloidal silica and silicates do not abstract and concentrate the salts from neutral salt solutions when filtered thru soils. Any such apparent effect is due, he believes, to a redistribution of the salt in the solution between the water of the colloid and the water of the solution.

Joly (1902–04), Briggs and Lapham (1902), and Dittrich in 1903 (cited by Sullivan, 1907:26) also have presented data tending to show that the action of neutral salt solutions on soils consists in an equivalent exchange of bases.

Ruprecht and Morse (1917) report the presence of soluble salts of iron, aluminium, and manganese in soils repeatedly dressed with ammonium sulfate without the addition of lime.

It thus appears that neutral salts of potassium when added to the soil are strongly absorbed, thus resulting in the liberation of other bases which may have either beneficial or harmful effects on plant growth. These effects may be due to some direct effect of the replaced bases on the plant's activities, or they may be induced indirectly by the modification of some of the soil's properties.

CONCLUSIONS

It appears from this summary of the literature that the common fertilizer salts of potassium have usually been found to exert harmful effects on plant growth only when used in large quantities. These effects may be accounted for in part by basic exchange, in which case the composition of the soil would be an important factor. Significant modifications of the bacterial activities in the soil may be another factor. In the following pages are reported the results of experimental work which was designed to throw light on these problems.

EXPERIMENTAL WORK

SOILS USED

Three soils were used in the experiments here reported — Hagerstown silt loam, Dekalb silt loam, and Volusia silt loam.

Hagerstown silt loam is a residual soil derived from limestone. It is known as a productive soil, and has good surface drainage and good underdrainage. The sample was collected near State College, Pennsylvania, from an old field which had never been fertilized in so far as could be learned. In collecting the soil the immediate surface was scraped off and the soil was taken to a depth of eight inches.

Dekalb silt loam is a residual soil derived from sandstone and shale. Its productivity is considered as poor to medium. It is typically poorly underdrained. The sample was collected from an abandoned field near Snow Shoe, Pennsylvania, in the same manner as was the Hagerstown silt loam.

Volusia silt loam is a glacial soil composed of a small proportion of glacial material mixed with soil material derived from local sandstone and shale. There is such a wide variation in this soil that it cannot be characterized as a series. The sample was collected near Ithaca, New York, from an unproductive, poorly underdrained field, the same method being used as was used in collecting the other soils.

PREPARATION OF THE SOILS

The soil samples were brought to the laboratory and immediately screened thru a 4-millimeter screen. Small samples of the screened soils were taken for moisture and acidity determinations, and pots were filled with a known weight of the soil calculated to the water-free basis. After the pots were filled, the contents of each pot were emptied on an oilcloth, the required quantity of precipitated calcium carbonate and potassium salt was added and thoroly mixed with the soil, and the pot was refilled. In the case of the Volusia soil, the potassium salt was added in solution after the calcium carbonate had been mixed with the soil and the pot had been refilled. The pots were then brought to weight with distilled water. Sufficient calcium carbonate was added to the Hagerstown and Dekalb soils to just satisfy their lime requirement, which amounted to 2 tons of calcium carbonate to 2,000,000 pounds of soil in each case.

With the Volusia soil varying amounts of the carbonate were used, as follows: Series I — no lime, lime requirement 3393 pounds of calcium carbonate to 2,000,000 pounds of soil; Series II — lime requirement just satisfied; Series III — 2 tons of calcium carbonate to 2,000,000 pounds of soil in excess of the lime requirement.

PLAN OF THE EXPERIMENTAL WORK

On the Hagerstown and Dekalb soils no crop was grown the first year. Composite samples of each treatment, in triplicate, were taken for nitrate determinations, with a $\frac{3}{4}$-inch brass tube, the day after bringing the pots to weight and at regular intervals thereafter during the first year. The moisture content was maintained at approximately 24 per cent (water-free basis) by bringing the pots to weight weekly with distilled water.

TABLE 1. TREATMENTS OF HAGERSTOWN AND DEKALB SILT LOAM SOILS
(Lime requirement of soils just satisfied; moisture content maintained at 24 per cent)

Pot	Pounds of potassium salt to 2,000,000 pounds of soil	
	KCl	K_2SO_4
1 {a, b, c}	0	0
2 {a, b, c}	200	200
3 {a, b, c}	500	500
4 {a, b, c}	1,000	1,000
5 {a, b, c}	2,000	2,000
6 {a, b, c}	3,000	3,000

The following year the triplicates were thoroly mixed on oilcloth, duplicate pots were filled with each treatment, and wheat was planted and grown to maturity thru the winter and spring. At the time of making up the duplicate pots, samples were taken, air-dried, and stored to be used later in determining the effect of treatment on water-soluble bases and on the growth of wheat seedlings in the water extracts of the soils.

TABLE 2. TREATMENTS OF VOLUSIA SILT LOAM
(Moisture content maintained at 30 per cent)

Series 1 — No $CaCO_3$; lime requirement 3393 pounds $CaCO_3$ to 2,000,000 pounds of soil

Pot	Pounds of KCl to 2,000,000 pounds of soil	Number of pots	
		Cropped to wheat	No crop grown
1	0	4 1-gallon	1 3-gallon
2	200	4 1-gallon	1 3-gallon
3	500	4 1-gallon	1 3-gallon
4	1,000	4 1-gallon	1 3-gallon
5	2,000	4 1-gallon	1 3-gallon

Series II — Same plan as Series I, with lime requirement just satisfied

Series III — Same plan as Series I, with 4000 pounds of $CaCO_3$ to 2,000,000 pounds of soil in excess of lime requirement

In the case of the Volusia soil, quadruplicate 1-gallon pots were made up of each treatment, to be cropped to wheat, and one 3-gallon pot in each treatment was filled to be used later in the other studies. All of these pots were brought to weight weekly (30 per cent moisture content, water-free basis) with distilled water. All of the laboratory determinations, including soil extract cultures with wheat seedlings, were made on samples from the 3-gallon pots, which had been kept in the greenhouse under the same conditions as the cropped pots and maintained at an approximately constant moisture content for about seven months.

The outline given in tables 1 and 2 makes the plan of the work clear.

EXPERIMENTAL METHODS

Pot cultures

Two-gallon pots were used with the Hagerstown and Dekalb soils, each pot containing the equivalent of $9\frac{1}{4}$ pounds of water-free soil. One-gallon pots were used with the Volusia soil, each pot containing the equivalent of 6 pounds of water-free soil. Duplicate pots were used with the Hagerstown and Dekalb soils, and quadruplicate pots with the Volusia soil. The Hagerstown and Dekalb soils were maintained at a moisture content of 24 per cent, water-free basis, and the Volusia soil at 30 per cent. These moisture contents gave approximately two-thirds saturation.

Soil extract cultures

Soil extract.— The soil extract for the solution cultures and the analyses for water-soluble bases was prepared by adding five parts of water to one part of soil (after correcting for the water already in the soil), shaking for three hours, and immediately filtering thru Pasteur-Chamberland filters.

Analysis of extract.— The official methods of analysis of the United States Bureau of Chemistry[1] were used, with the following exceptions: Manganese was determined by the ammonium persulfate method as described by Hillebrand (1910). Calcium was precipitated according to the official method, and titrated with potassium permanganate after solution in dilute sulfuric acid.

Soil extract cultures.— The soil extract cultures were run in duplicate. Erlenmeyer flasks of 500 cubic centimeters capacity were used for culture vessels. Four wheat plants were grown in each flask by using a paraffined paper cover thru which four holes were punched to receive the rootlets. The plants were allowed to grow for four weeks. They were then removed, photographs were taken of the roots, and the dry weights were determined.

Nitrification

In the nitrification trials, tumblers were used for containers and 100 grams of soil was placed in each tumbler. Three nitrifiable materials — ammonium sulfate, ammonium hydroxide, and dried blood — were used.

[1] Official and provisional methods of analysis, Association of Official Agricultural Chemists. U. S. Bur. Chem., Bul. 107. 1912.

The ammonium sulfate and the ammonium hydroxide were applied in dilute solution, and the dried blood was well mixed with the soil on a piece of oilcloth. The cultures were incubated at room temperature and were brought to weight every six days with distilled water. Excessive evaporation was prevented by covering the tumblers with a layer of cotton placed between pieces of cheesecloth. The period of incubation, percentage of moisture maintained, and nitrifiable material used, are shown with each table in which the results are given.

Nitrates were determined by the phenoldisulphonic-acid method as described by Schreiner and Failyer (1906).

Soil acidity determination

The lime requirement of the soils was determined by a modified Veitch method (White, 1914).

EXPERIMENTAL RESULTS

Pot cultures

The crop on the Hagerstown and Dekalb soils was attacked by sparrows on the afternoon of the day before it had been intended to harvest the pots, and as a result only the yield of straw is given. In the case of the Volusia soil, the probable error of the average for the quadruplicate pots is so high as to render most of the possible comparisons of questionable value. The probable errors were computed by means of Peter's formula as given by Mellor (1909),

$$R = \pm\ 0.8453 \frac{\Sigma\,(+v)}{n\sqrt{n-1}}$$

in which Σ (+ v) denotes the sum of the deviations of each observation from the mean, disregarding their sign, and n denotes the number of observations made.

The results of the pot experiments are given in tables 3 and 4.

Potassium sulfate increased the yield of straw over the check in both the Hagerstown and the Dekalb soil. In the Hagerstown soil there was a continued increase in yield with an increase in the rate of application after 500 pounds was reached. In the case of the Dekalb soil the data are not conclusive, except that, as with the Hagerstown soil, there is no evidence of a toxic condition with any of the treatments.

TABLE 3. YIELD OF WHEAT STRAW IN POT CULTURES WITH HAGERSTOWN AND DEKALB SILT LOAMS

(Lime requirement of soils just satisfied)

Pot	Pounds of K_2SO_4 to 2,000,000 pounds of soil	Yield of straw in grams		Pounds of KCl to 2,000,000 pounds of soil	Yield of straw in grams	
		Duplicates	Average		Duplicates	Average
			Hagerstown silt loam			
1	0	4.36, 4.25	4.31	0	4.12, 4.18	4.15
2	200	5.56, 5.26	5.41	200	4.45, 4.37	4.41
3	500	5.02, 5.15	5.09	500	4.87, 4.07	4.47
4	1,000	6.70, 4.85	5.77	1,000	3.91, 3.95	3.93
5	2,000	6.50, 5.65	6.08	2,000	3.86, 4.02	3.94
6	3,000	6.69, 6.16	6.43	3,000	3.11, 3.41	3.26
			Dekalb silt loam			
1	0	1.85, 1.87	1.86	0	2.02, 1.87	1.95
2	200	1.82, 1.92	1.87	200	1.98, 1.83	1.91
3	500	1.83, 1.88	1.86	500	1.73, 1.85	1.79
4	1,000	1.59, 1.71	1.65	1,000	1.98, 1.90	1.94
5	2,000	2.08, 1.88	1.98	2,000	1.71, 1.65	1.68
6	3,000	2.01, 2.10	2.06	3,000	1.70, 1.66	1.68

Potassium chloride apparently became toxic at the 1000-pound treatment with the Hagerstown soil and at the 2000-pound treatment with the Dekalb soil. The data, however, are not conclusive, and warrant only tentative conclusions regarding the rate of application necessary to bring about a toxic condition in these soils.

TABLE 4. YIELD OF WHEAT STRAW AND GRAIN IN POT CULTURES WITH VOLUSIA SILT LOAM

Series	Pounds of KCl to 2,000,000 pounds of soil	Straw (average of quadruplicates, in grams)	Grain (average of quadruplicates, in grams)
I No lime; lime requirement 3393 pounds $CaCO_3$ to 2,000,000 pounds of soil	0	6.3 ± 0.41	3.03 ± 0.10
	200	6.5 ± 0.45	3.14 ± 0.18
	500	6.6 ± 0.40	3.17 ± 0.13
	1,000	6.7 ± 0.14	3.22 ± 0.13
	2,000	8.6 ± 0.44	3.85 ± 0.19
II Lime requirement just satisfied	0	8.8 ± 0.85	4.09 ± 0.62
	200	7.2 ± 0.37	3.46 ± 0.30
	500	6.6 ± 0.23	2.79 ± 0.13
	1,000	7.4 ± 0.13	3.12 ± 0.12
	2,000	7.9 ± 0.13	3.59 ± 0.05
III 4000 pounds $CaCO_3$ to 2,000,000 pounds of soil in excess of lime requirement	0	12.1 ± 0.76	6.06 ± 0.68
	200	13.4 ± 0.53	5.13 ± 0.66
	500	10.7 ± 0.22	2.80 ± 0.44
	1,000	15.5 ± 2.45	5.18 ± 0.64
	2,000	11.9 ± 0.33	4.14 ± 0.12

Soil extract cultures

Both the root and the top growth of the wheat seedlings were very uniform in the duplicate water extract cultures. The dry weights, however, while uniform between duplicates, did not give a good measure of the comparative root growth between cultures, and consequently are not reported.

The presence of some toxic substance or substances in certain of the cultures is indicated in figures 161 to 163. The sensitiveness of the roots of seedlings to toxic substances has been adequately demonstrated by Schreiner and his associates in the United States Bureau of Soils, and by Breazeale and LeClerc, of the Laboratory of Plant Physiology of the United States Department of Agriculture.

In the extract from the Hagerstown soil (fig. 161) the chloride is seen to have stimulated root growth thruout the series, the greatest degree of stimulation resulting from the 500-pound treatment. In the sulfate series there is seen a progressive stimulation of root growth up to the

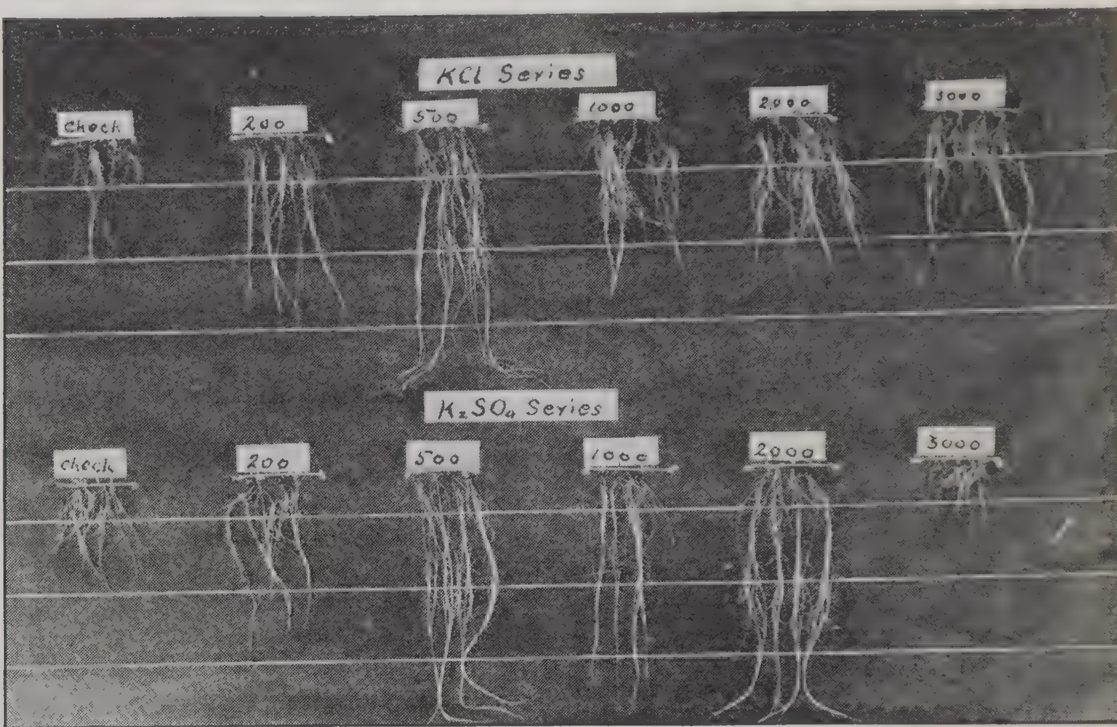

Fig. 161. ROOT GROWTH OF WHEAT SEEDLINGS IN WATER EXTRACTS FROM HAGERSTOWN SILT LOAM WHICH HAD RECEIVED VARYING AMOUNTS OF THE CHLORIDE AND THE SULFATE OF POTASSIUM

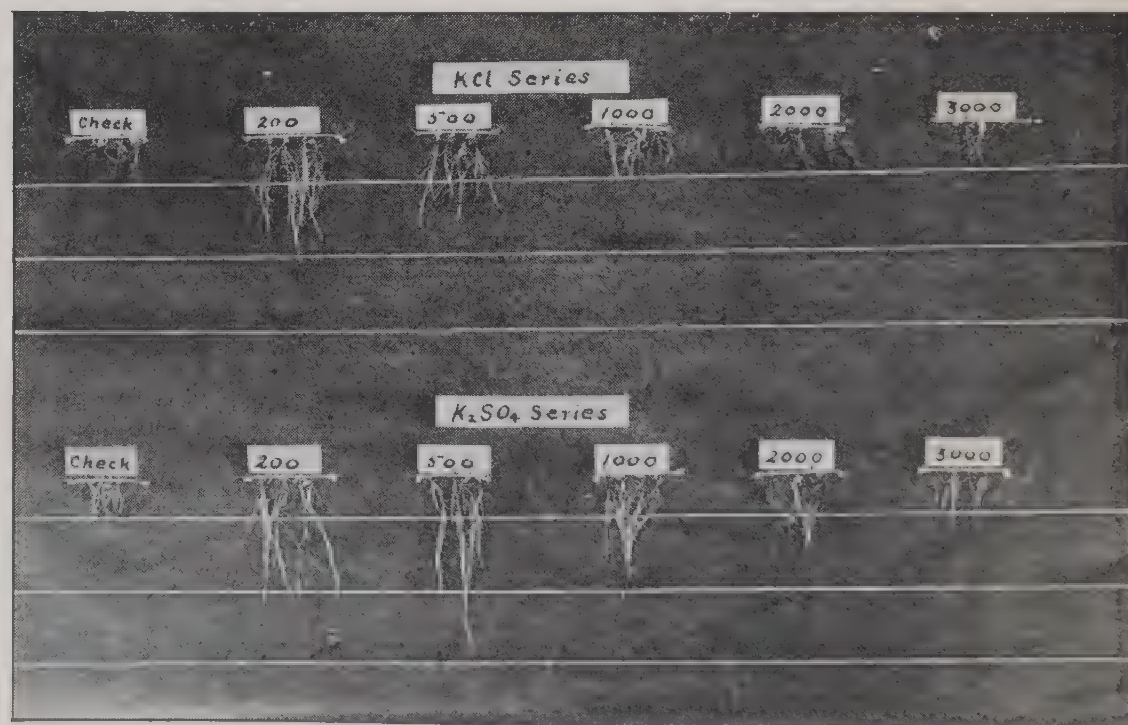

Fig. 162. ROOT GROWTH OF WHEAT SEEDLINGS IN WATER EXTRACTS FROM DEKALB SILT LOAM WHICH HAD RECEIVED VARYING AMOUNTS OF THE CHLORIDE AND THE SULFATE OF POTASSIUM

2000-pound treatment, and a marked toxicity with the 3000-pound treatment. These latter results agree in the main with the yield of straw in the pot cultures except in the case of the heaviest sulfate treatment. In this case the extract cultures showed strong toxicity, while no such condition was present in the pot cultures.

In the extract from the Dekalb soil (fig. 162) no distinct toxicity was shown in any of the cultures when compared to the checks. The checks, however, were apparently toxic. With the chloride the 200-pound treat-

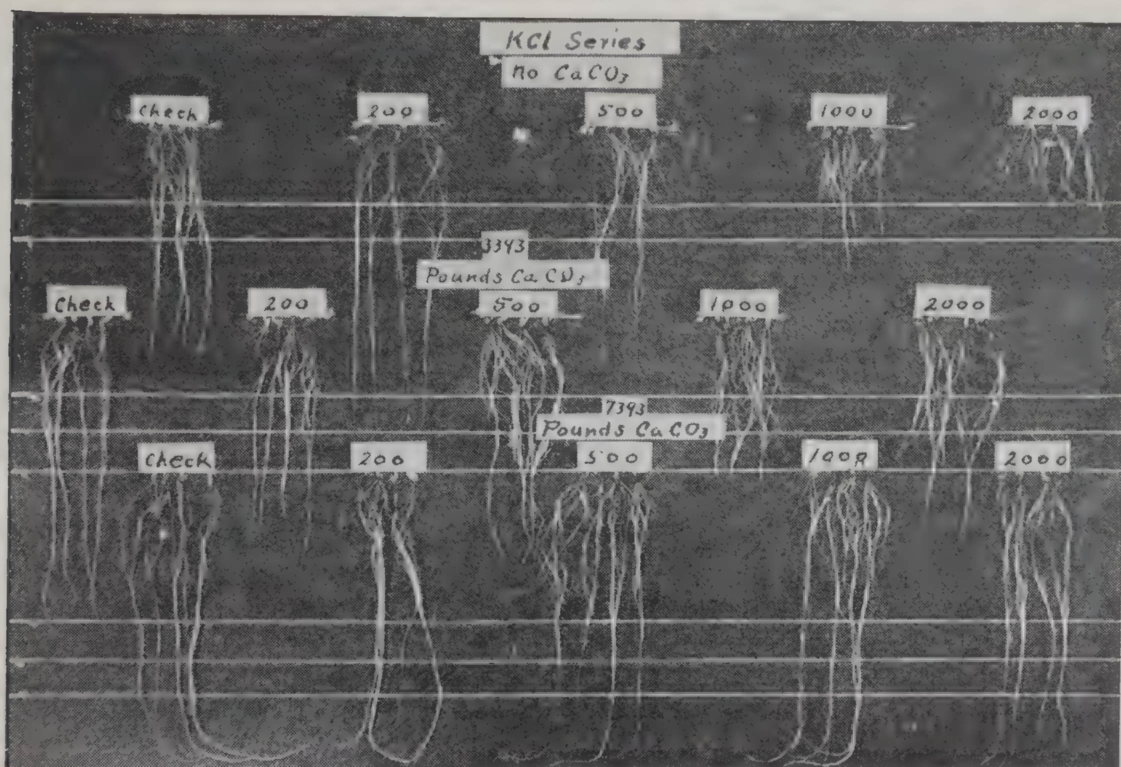

FIG. 163. ROOT GROWTH OF WHEAT SEEDLINGS IN WATER EXTRACTS FROM VOLUSIA SILT LOAM WHICH HAD RECEIVED VARYING AMOUNTS OF POTASSIUM CHLORIDE, BOTH WITH AND WITHOUT LIME

ment caused the greatest stimulation of root growth, while with the sulfate there was little difference between the degree of stimulation in the 200- and the 500-pound treatments. These results are not reflected in the yields from the pot cultures. The yields from the pots were very small and the final weights are probably not a good index of the relative vigor of growth.

In the Volusia extract cultures (fig. 163) the important point brought out is the neutralization of the toxic condition by the calcium carbonate.

A distinctly toxic condition was evident in the no-lime series with the heavier chloride treatments. This condition was less pronounced in the series receiving enough lime to just meet the lime requirement of the soil, and almost entirely disappeared when 4000 pounds of lime to 2,000,000 pounds of soil in excess of the lime requirement of the soil was used.

Nitrification

As a measure of the activity of the nitrifying organisms in the variously treated soils, determinations were made of the nitrates accumulated over long periods of time and of the nitrification of added materials. The accumulation of nitrates in the three soils used is shown in tables 5, 6, and 7, respectively. The figures represent the milligrams of nitrate nitrogen in 100 grams of soil as determined when the pots were set up and at stated intervals thereafter. The difference between the initial nitrate content and that after a given interval represents the actual

TABLE 5. ACCUMULATION OF NITRATES IN HAGERSTOWN SILT LOAM AS DETERMINED AT INTERVALS AFTER THE EXPERIMENT WAS SET UP

(Moisture content, 24 per cent)

Pounds of potassium salt to 2,000,000 pounds of soil	Milligrams of nitrogen as nitrates in 100 grams of soil			
	At time of setting up experiment	After 33 days	After 61 days	After 86 days
(KCl)				
0	1.90	2.50	3.33	3.10
200	2.12	1.86	3.07	2.86
500	1.66	1.80	2.91	3.05
1,000	1.50	1.94	2.82	2.94
2,000	Trace	2.09	3.02	2.82
3,000	1.41	2.04	3.26	2.83
(K_2SO_4)				
0	1.53	2.06	3.88	3.87
200	1.96	2.53	3.22	3.60
500	1.68	2.83	3.65	3.35
1,000	1.69	2.61	3.89	4.06
2,000	2.15	2.53	3.81	4.40
3,000	1.46	2.54	3.97	4.48

accumulation, or, in some cases, loss. In the case of the Volusia soil, nitrate accumulation was determined but once, after a seven-months period.

TABLE 6. ACCUMULATION OF NITRATES IN DEKALB SILT LOAM AS DETERMINED AT INTERVALS AFTER THE EXPERIMENT WAS SET UP

(Moisture content, 24 per cent)

Pounds of potassium salt to 2,000,000 pounds of soil	Milligrams of nitrogen as nitrates in 100 grams of soil			
	At time of setting up experiment	After 33 days	After 61 days	After 86 days
(KCl)				
0	Trace	0.65	1.14	1.69
200	Trace	0.40	0.92	1.36
500	Trace	0.49	1.04	1.56
1,000	Trace	0.68	0.91	1.44
2,000	Trace	0.36	0.60	1.27
3,000	Trace	Trace	0.49	0.69
(K_2SO_4)				
0	Trace	0.71	1.44	1.25
200	Trace	0.70	1.31	1.97
500	Trace	0.67	1.65	2.27
1,000	Trace	0.89	1.86	2.71
2,000	Trace	0.81	2.13	2.16
3,000	Trace	0.63	1.87	2.08

It will be noted that in every case the potassium chloride decreased the accumulation of nitrates, and that the depression increased regularly with an increase in the amount of chloride applied except for one or two minor exceptions. In the Volusia soil the degree of depression with the heavy chloride treatments was less in the lime series than in the no-lime series, indicating the tendency of the lime to overcome the harmful effects of the potassium chloride.

Potassium sulfate seems to have exerted a stimulating effect on nitrate accumulation. In the Dekalb soil the greatest degree of stimulation occurs with the 1000-pound treatment, and then there is a gradual decline with the two heavier treatments.

TABLE 7. Accumulation of Nitrates in Volusia Silt Loam after Seven Months
(Moisture content, 30 per cent)

Series	Pounds of KCl to 2,000,000 pounds of soil	Milligrams of nitrogen as nitrates in 100 grams of soil	
		At time of setting up experiment	After seven months
I No lime; lime requirement 3393 pounds $CaCO_3$ to 2,000,000 pounds of soil	0	2.00	6.06
	200	2.00	5.55
	500	2.00	4.88
	1,000	2.00	3.77
	2,000	2.00	2.32
II Lime requirement just satisfied	0	2.00	7.50
	200	2.00	7.14
	500	2.00	5.97
	1,000	2.00	4.81
	2,000	2.00	4.08
III 4000 pounds $CaCO_3$ to 2,000,000 pounds of soil in excess of lime requirement	0	2.00	9.76
	200	2.00	9.09
	500	2.00	8.69
	1,000	2.00	7.01
	2,000	2.00	6.45

With the twenty-one-days incubation period (tables 8 to 10), all of the soils in which the lime requirement was just satisfied show the initial depression of nitrification with the 1000-pound treatment of the chloride. When ammonium hydroxide was the nitrifiable material added (table 10), altho the initial depression occurred at this point the nitrates found in the heaviest chloride treatment exceeded those in the check, indicating perhaps some action due to the basic nature of the hydroxide.

In the Hagerstown soil treated with potassium sulfate (table 8), nitrification was depressed slightly below that in the check with the heaviest sulfate treatment. This was not the case in the Dekalb soil (table 9), altho in the latter soil the 3000-pound treatment caused less stimulation of the process than did the 2000-pound treatment.

TABLE 8. NITRIFICATION IN HAGERSTOWN SILT LOAM WHEN AMMONIUM SULFATE IS USED

(Moisture content, 24 per cent; incubation period, 21 days)

Pounds of potassium salt to 2,000,000 pounds of soil	Nitrogen as nitrates in 100 grams of soil		Nitrogen in $(NH_4)_2SO_4$ nitrified	
	Check (milligrams)	21.2 milligrams N added (milligrams)	Milligrams	Per cent
(KCl)				
0	3.11	13.98	10.87	51.27
200	2.86	14.42	11.56	54.52
500	3.05	14.93	11.88	56.03
1,000	2.94	12.95	10.01	47.21
2,000	2.82	10.94	8.12	38.30
3,000	2.83	8.28	5.45	25.70
(K_2SO_4)				
0	3.87	17.18	13.31	62.31
200	3.60	16.80	13.20	62.26
500	3.35	17.52	14.17	66.83
1,000	4.06	19.03	14.97	70.61
2,000	4.40	21.60	17.20	81.13
3,000	4.48	17.64	13.16	62.07

TABLE 9. NITRIFICATION IN DEKALB SILT LOAM WHEN AMMONIUM SULFATE IS USED

(Moisture content, 24 per cent; incubation period, 21 days)

Pounds of potassium salt to 2,000,000 pounds of soil	Nitrogen as nitrates in 100 grams of soil		Nitrogen in $(NH_4)_2SO_4$ nitrified	
	Check (milligrams)	21.2 milligrams N added (milligrams)	Milligrams	Per cent
(KCl)				
0	1.69	3.75	1.76	8.30
200	1.36	3.49	2.13	10.04
500	1.56	4.28	2.72	12.83
1,000	1.44	3.61	2.17	10.23
2,000	1.27	2.21	0.94	4.43
3,000	0.67	1.21	0.52	2.45
(K_2SO_4)				
0	1.25	3.62	2.37	11.17
200	1.97	3.58	1.61	7.59
500	2.27	4.76	2.49	11.74
1,000	2.71	5.55	2.84	13.39
2,000	2.16	5.74	3.58	16.88
3,000	2.08	4.82	2.74	12.92

The beneficial action of lime is again brought out in table 10. Here it is shown that in the no-lime series depression in the nitrification of ammonium hydroxide accompanied the application of potassium chloride. When the lime requirement of the soil was just satisfied, the initial depression occurred with the 1000-pound treatment, and when lime was used in excess of the lime requirement the initial depression occurred with the 2000-pound treatment.

TABLE 10. NITRIFICATION IN VOLUSIA SILT LOAM WHEN AMMONIUM HYDROXIDE IS USED

(Moisture content, 30 per cent; incubation period, 21 days)

Series	Pounds of KCl to 2,000,000 pounds of soil	Nitrogen as nitrates in 100 grams of soil		Nitrogen in NH_4OH nitrified	
		Check (milligrams)	21.2 milligrams N added (milligrams)	Milligrams	Per cent
I No lime; lime requirement 3393 pounds of $CaCO_3$ to 2,000,000 pounds of soil	0	6.65	8.19	1.94	4.73
	200	5.88	7.41	1.53	3.73
	500	4.88	6.25	1.37	3.34
	1,000	4.54	6.00	1.46	3.56
	2,000	2.70	3.50	0.80	1.95
II Lime requirement just satisfied	0	7.69	11.11	3.42	8.34
	200	5.58	10.96	5.38	13.12
	500	5.33	12.50	7.17	17.48
	1,000	5.12	10.77	5.65	13.78
	2,000	3.33	7.41	4.08	9.95
III 4000 pounds of $CaCO_3$ to 2,000,000 pounds of soil in excess of lime requirement	0	11.11	17.02	5.91	14.41
	200	11.11	20.00	8.89	21.68
	500	9.20	20.00	10.80	26.34
	1,000	8.00	19.52	11.52	28.10
	2,000	7.41	16.02	8.61	21.00

The results from the use of dried blood as the nitrifiable material are given in table 11. Here again the beneficial action of lime in counteracting the ill effects of potassium chloride is shown very strongly. It is possible that a longer incubation period would have allowed more nitrification in Series I. An acid condition is apparently very unfavorable to the nitrification of dried blood.

TABLE 11. Nitrification in Volusia Silt Loam When Dried Blood Is Used
(Moisture content, 20 per cent; incubation period, 14 days)

Series	Pounds of KCl to 2,000,000 pounds of soil	Nitrogen as nitrates in 100 grams of soil		Nitrogen in blood nitrified	
		Check (milli-grams)	21.2 milli-grams N added (milli-grams)	Milli-grams	Per cent
I No lime; lime requirement 3352 pounds of $CaCO_3$ to 2,000,000 pounds of soil	0	7.69	7.84	0.15	0.71
	200	7.76	7.14	0.00	0.00
	500	6.25	5.88	0.00	0.00
	1,000	4.54	4.66	0.12	0.57
	2,000	3.57	3.17	0.00	0.00
II Lime requirement just satisfied	0	8.60	10.98	2.38	11.23
	200	8.00	10.00	2.00	9.52
	500	7.41	8.69	1.28	6.06
	1,000	5.63	7.47	1.84	8.76
	2,000	4.60	5.08	0.48	2.19
III 4700 pounds of $CaCO_3$ to 2,000,000 pounds of soil in excess of lime requirement	0	11.59	21.54	9.95	47.38
	200	11.11	21.27	[illegible]	[illegible]
	500	9.63	20.58	10.95	52.13
	1,000	8.42	18.64	[illegible]	[illegible]
	2,000	7.76	16.08	[illegible]	[illegible]

Another series was run with Volusia soil, using ammonium hydroxide and incubating for fourteen days. The results of this series are not included herein, for they simply confirm the results of the twenty-one-days incubation period.

In the foregoing discussion of the nitrifying power of the variously treated soils, it has been assumed that the increase in nitrates during the incubation period was due entirely to the oxidation of the added materials. This assumption is clearly not entirely justified, and yet any other method of obtaining the desired information would probably be open to equally serious criticism.

Interchange of bases

The marked influence of potassium chloride on the nitrate bacteria raised the question as to whether the toxic effect might be due to replaced

bases. With this possibility in view, the water extracts of the variously treated soils were tested for calcium, iron, aluminium, magnesium, and manganese, and when found to be present each of these elements was determined quantitatively.

No iron nor aluminium was found in any of the extracts, and no manganese nor magnesium was found in certain of them, as appears in tables 12 to 15. All determinations were made in duplicate, and checked very closely, so that only the averages are given.

TABLE 12. AMOUNTS OF CALCIUM IN VARIOUSLY TREATED SOILS

Pounds of potassium salt to 2,000,000 pounds of soil	Parts of calcium per million parts of soil extract				
	Hagerstown	Dekalb	Volusia		
	Lime requirement just satisfied	Lime requirement just satisfied	No lime; lime requirement 3393 lbs. $CaCO_3$	Lime requirement just satisfied	Lime 4000 lbs. in excess of requirement
(KCl)					
0	21.6	2.9	15.1	27.7	33.6
200	30.5	5.7	15.9	26.7	40.7
500	34.8	6.1	23.2	28.5	46.2
1,000	44.2	6.5	26.5	44.8	54.3
2,000	60.3	11.6	38.4	51.4	53.7
3,000	72.2	13.0	....	....	....
(K_2SO_4)					
0	21.1	2.1	....	....	....
200	24.1	3.8	....	....	....
500	25.2	3.8	....	....	....
1,000	29.5	4.5	....	....	....
2,000	36.7	5.5	....	....	....
3,000	45.1	6.0	....	....	....

As shown in table 12, with equal (but not equivalent) weights of the chloride and the sulfate of potassium the chloride replaced more calcium than did the sulfate. This result is to be expected, since equal weights of the two salts do not carry equal weights of the base.

As has been noted, Peters (1860) and Küllenberg (1867) both found that the base entered into the reaction independently of its form of combination. It does not follow from this, however, that equivalent weights

of the bases in a soil would appear in the extracts from the same soil treated with various acids of the same base, because of the different solubilities of the products of the reactions. Calcium sulfate is less soluble than calcium chloride, and consequently less calcium would probably be found in the extract of a soil treated with the sulfate than in one treated with the chloride of potassium. This is apparently the condition that existed in these soils, for there is less calcium present in the extracts from the sulfate treatments than should be present theoretically if the relative solubilities are discarded and only the replacing power of the potassium actually added is considered.

No magnesium was found in any of the extracts from the Volusia soil. This series is reported by Robinson (1914) to be low in magnesium. In the Hagerstown and Dekalb soils (table 13), less magnesium than calcium was replaced by potassium. This result is in accord with results from previous work.

TABLE 13. AMOUNTS OF MAGNESIUM IN VARIOUSLY TREATED SOILS

Pounds of potassium salt to 2,000,000 pounds of soil	Parts of magnesium per million parts of soil extract	
	Hagerstown	Dekalb
	Lime requirement just satisfied	Lime requirement just satisfied
(KCl)		
0	15.6	2.9
200	18.0	3.5
500	19.4	3.7
1,000	21.2	3.7
2,000	24.8	5.0
3,000	26.2	5.7
(K_2SO_4)		
0	12.8	2.5
200	15.0	2.5
500	15.8	2.5
1,000	16.8	2.2
2,000	18.0	2.7
3,000	19.6	2.8

That appreciable amounts of manganese went into solution in the Hagerstown and Dekalb soils is indicated in table 14. As previously noted, manganese has been found to be strongly toxic both to plant growth and to nitrification. Skinner and Reid (1916), as already stated, found

TABLE 14. AMOUNTS OF MANGANESE IN VARIOUSLY TREATED SOILS

Pounds of potassium salt to 2,000,000 pounds of soil	Parts of manganese per million parts of soil extract				
	Hagerstown	Dekalb	Volusia		
	Lime requirement just satisfied	Lime requirement just satisfied	No lime; lime requirement 3393 lbs. $CaCO_3$	Lime requirement just satisfied	Lime 4000 lbs. in excess of requirement
(KCl)					
0	0.24	0.78	0.00	0.00	0.00
200	0.47	1.11	0.00	0.00	0.00
500	0.57	1.92	Trace	0.00	0.00
1,000	0.71	3.12	0.30	0.00	0.00
2,000	1.15	4.17	0.65	Trace	0.00
3,000	1.64	6.25	......	......	......
(K_2SO_4)					
0	0.93	0.50	......	......	......
200	0.99	0.53	......	......	......
500	1.44	0.83	......	......	......
1,000	2.03	1.08	......	......	......
2,000	2.35	1.78	......	......	......
3,000	2.80	2.50	......	......	......

that manganese chloride was distinctly harmful to crop growth in an acid soil when used at the rate of 50 pounds to the acre. This application would be equivalent to about 14 parts of manganese to 1,000,000 parts of soil if it is assumed that the salt became mixed with the surface soil only. The Dekalb soil showed approximately this concentration of manganese when its extract became toxic to wheat seedlings. To bring this out more clearly, the parts per million of manganese in dry soil are calculated in table 15.

The presence of manganese, however, cannot be considered as a complete explanation for the toxic condition found in the extract cultures

and indicated in the pot cultures, and for the depression of nitrification particularly with the chloride treatments. The extract from the Volusia soil was toxic to wheat seedlings in certain treatments and no manganese was found in solution. Toxicity in solution cultures may arise from a number of conditions, one of which is a lack of balance of nutrients. It is of interest, nevertheless, tho perhaps not of significance, to note that the soil having the highest content of water-soluble manganese showed the weakest nitrifying power and the smallest accumulation of nitrates, as well as the smallest growth of wheat in pot cultures and of wheat roots in extract cultures.

TABLE 15. AMOUNT OF MANGANESE IN DRY SOIL

Pounds of potassium salt to 2,000,000 pounds of soil	Parts per million of water-soluble manganese in dry soil	
	Hagerstown	Dekalb
	Lime requirement just satisfied	Lime requirement just satisfied
(KCl)		
0	1.20	3.90
200	2.35	5.55
500	2.85	9.60
1,000	3.55	15.60
2,000	5.75	20.85
3,000	8.20	31.25
(K_2SO_4)		
0	0.93	2.50
200	0.99	2.65
500	1.44	4.65
1,000	2.03	5.42
2,000	2.35	8.92
3,000	2.80	12.50

SUMMARY

Three silt loam soils were used in the experiments reported herein, each soil being representative of a large area in the United States. The productivity of the soils ranged from high to very low.

The soils were screened and the pots were filled with the treated soils as described. The official methods of analysis of the United States Bureau of Chemistry were used, with the exceptions noted.

Potassium sulfate increased the yield of straw in Hagerstown soil and showed no toxic effect in Dekalb soil. Potassium chloride apparently became toxic to wheat in Hagerstown soil with the 1000-pound application; in the Dekalb soil there was a slight decrease in yield with the 2000-pound treatment.

In the extracts from the Hagerstown soil, potassium chloride stimulated the root growth of wheat seedlings at all concentrations, the greatest stimulation occurring with the 500-pound treatment. With the sulfate there was a progressive stimulation to the 2000-pound treatment, and a marked toxicity with the 3000-pound treatment. In the extracts from the Dekalb soil the checks were toxic to the root growth of wheat seedlings. With the chloride the 200-pound treatment caused the greatest stimulation, and there was a decrease in stimulation and apparent toxicity with the heavier treatments. With the sulfate the 500-pound treatment caused the greatest stimulation, and there was a decrease in stimulation and apparent toxicity with the heavier treatments. In the extracts from the no-lime series of the Volusia soil, toxicity to root growth became evident with the 500-pound treatment. Lime overcame the toxicity even with the heaviest chloride treatment.

Potassium chloride decreased the accumulation of nitrates in all cases. Lime overcame this effect in part. Potassium sulfate apparently stimulated the accumulation of nitrates in Hagerstown and Dekalb soils.

The heavier potassium chloride treatments depressed nitrification of added materials. Potassium sulfate stimulated the process in all three soils with the exception of the heaviest treatment with Hagerstown soil. Lime had a tendency to correct the depression of the chloride in the Volusia soil, but did not entirely overcome it.

No iron nor aluminium was found in any of the water extracts, and no manganese was found in the extracts from the Volusia soil; hence the harmful action of the potassium salts cannot be attributed to replaced iron or aluminium, or to manganese in the case of Volusia soil. Both the chloride and the sulfate of potassium replaced calcium strongly. Less calcium appeared in the extract from the sulfate-treated series than would be expected, possibly because of the relative insolubility of calcium

sulfate. Magnesium was replaced less strongly than was calcium. Manganese was replaced in very appreciable amounts in Hagerstown and Dekalb soil, particularly in the latter. The soil highest in water-soluble manganese showed the least nitrifying efficiency, the smallest growth of wheat in pot cultures, and the poorest growth of wheat rootlets in extract cultures.

The effects of potassium salts on plant growth are due to a complex interaction of factors, involving perhaps the direct action of the salts on plant growth and on bacterial activities, and also the action of bases replaced by the potassium, particularly manganese.

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RESISTANCE OF THE ROOTS OF SOME FRUIT SPECIES TO LOW TEMPERATURE

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CONTENTS

RESISTANCE OF THE ROOTS OF SOME FRUIT SPECIES TO LOW TEMPERATURE

RESISTANCE OF THE ROOTS OF SOME FRUIT SPECIES TO LOW TEMPERATURE [1]

D. B. Carrick

There are several types of winter injury to fruit plants which are of more or less frequent occurrence in New York State. Among these may be mentioned injury to small twigs, especially those of peach trees and of tender apple varieties such as Tompkins King; injury to the winter buds and sometimes to the blossoms; sun-scald, and the rather closely related forms of crotch injury and crown rot; and injury to the roots. Perhaps the killing of the roots by low temperature should be associated with the less serious types of winter injury in this State, due in part to the fact that it occurs in restricted areas. Yet in the Champlain Valley and in the upper Hudson River section, the freezing of the roots is one of the important problems in fruit production. This is also the case in parts of New England, in Canada, and in a number of the Western States.

The work reported in this paper was begun in the fall of 1915 and extended thru the spring of 1917. An attempt has been made to determine approximately under standard conditions the range of variation and the relative hardiness of some of the more commonly grown fruit stocks, including a few varieties of the small fruits. Some data were also obtained regarding the influence of certain factors on the freezing to death of plant tissue.

Careful field studies and the testing of possible fruit stocks capable of withstanding severe cold are significant aspects of the question that have not been attacked. It is hoped, however, that some of the results presented here may be suggestive in the working out of these other phases of the problem of root injury by low temperature.

REVIEW OF THE LITERATURE

Craig (1900) observed extensive winter injury to the roots of apple, plum, and cherry in Iowa. The one- and two-year-old apple trees in the

[1] Also presented to the Faculty of the Graduate School of Cornell University, in August, 1917, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

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nursery were almost completely destroyed. In the orchard, apple trees from three to fifteen years old, situated on a north slope on light soils and unprotected by snow or vegetation, suffered very severely. It was noted, however, that hardy varieties rooted from the scion often withstood the same cold that killed trees which were wholly on seedling roots. The varieties least injured were: first, Siberian crab apple; second, native crab apples and the Hibernal type of Russian apples; and third, varieties of western origin such as Northwestern.

The most resistant plum stock seemed to be *Prunus Besseyi*. No injury in any case was found in this species. *Prunus americana* was the next in resistance, being only slightly injured. Marianna roots were seriously damaged, while Peach and Myrobalan roots were entirely killed.

The hardiest cherry root observed was the Morello stock, which, except where exposed, escaped with slight injury. Trees in the nursery on Mazzard stock were practically a total loss, while those on the Mahaleb stock suffered less.

From the foregoing observations Craig concluded that the absence of snow or other protective covering during an unusually severe winter accounted for the very considerable root injury. To prevent a recurrence he advocated the use of desirable cover crops, the employment of the hardiest stocks available, and the deep planting of young trees, especially on the loess soils of the State.

Emerson (1903) conducted an interesting experiment to determine the influence of mulching and soil moisture on the freezing of roots. He filled seven boxes, 2 feet square and 18 inches deep, with a loam soil, and planted twenty-five apple seedlings in each box.

In the box protected by a 4-inch straw mulch, there was a soil moisture content of 16 per cent. By this treatment no roots were found dead and but seven were injured. In the box covered occasionally with snow and containing 15.8 per cent of moisture, seven roots were dead and eight were injured. In the unprotected boxes the injury seemed to vary inversely with the increased water content of the soil. With 10.4 per cent of moisture the roots of twenty trees were dead and five were uninjured; with 25.6 per cent of moisture, eight roots were dead, four were injured, and thirteen were uninjured. Not a root was injured in a box stored in a cool, dry place, altho its soil contained only 10 per cent of moisture.

Emerson (1906) found some striking differences in the protection of certain cover crops against deep freezing. In one case in which the snow was held, the ground froze to a depth of six inches where corn was planted, twelve inches with a heavy cover of oats, fifteen inches under a medium heavy crop of millet, and twenty-four inches where the soil was bare. These facts suggest the use of cover crops which will catch and hold the snow in regions where root injury is prevalent.

Macoun (1908) mentions the killing of roots as one of the ten forms of winter injury occurring in Canada. He recommends the use of cover crops as a means of increasing the soil moisture and holding the snow. His observations on the effect of soil moisture were similar to the experience of Emerson. He states also that the grafting of apples on the garden crab-apple trees has somewhat reduced the root injuries due to freezing.

By means of careful artificial freezings, Chandler (1913) obtained a considerable amount of interesting data on the relative hardiness of various fruit stocks. He found that the range of killing temperature of apple, peach, pear, and plum roots was from $-3°$ C. in summer to $-12°$ in late winter with rather rapid freezing. He compared the killing temperature of apple roots actively growing in the greenhouse with that of dormant ones in cold storage, in basement storage, and outside in frozen soil, respectively. The three dormant treatments showed little difference in resistance, but the active tissues killed at three centigrade degrees higher than did the dormant roots. Similar comparisons of peach and Marianna plum roots showed somewhat less variation between the conditions of growth and dormancy.

Chandler observed also a diminished hardiness in the roots farthest from the crown, apparently varying with their soil depth. He demonstrated further that in most cases the roots coming from the scions of Ben Davis apple trees were hardier than similar roots from French apple seedlings. An extended laboratory determination of the comparative resistance of Marianna and Myrobalan plum roots and Mahaleb and Mazzard cherry stocks strongly confirmed Craig's observations under orchard conditions.

Mix (1916), while studying sun-scald in the northern part of the Champlain Valley, New York, observed a great amount of winter injury in the roots of apple trees from one to twenty years old. The injured condition

seemed most serious where fall plowing was practiced and where the trees were on light soils and in windy situations. The Ben Davis trees were especially susceptible, from 50 to 75 per cent of these being left in a dying condition. Northern Spy and Wealthy trees also were injured, but in a degree much less than the Ben Davis. Mix observed also some cases in which, as he states, "the hardiness of the stock seems to have been influenced by the scion."

METHOD USED IN FREEZING THE ROOTS

The apparatus used in this study for freezing the roots consisted of: an inner chamber of galvanized iron 9 inches long, 1½ inches wide, and 30 inches deep; an outer chamber of the same material, 6 inches long, 12 inches wide, and of the same depth as the inner chamber; and around the outer chamber, 5 inches of insulation held in place by a casing of wood. The roots to be frozen were placed in the inner compartment, and were surrounded by the freezing mixture of ice and common salt in the second chamber. At no time was the actual tissue temperature determined, but the temperature of the air around the tissues was measured by means of three electrical resistance thermometers and a balance indicator. The latter instrument consisted of the circuit of a Wheatstone bridge mounted in a suitable case with a galvanometer and means for balancing the bridge by moving a contact along a slide wire.[2] The three electrical resistance bulbs, each with leads 5 feet long, were used until the variation in temperature in the lower part of the freezing chamber was determined. These bulbs were standardized by the makers and were carefully checked against one another in the laboratory here. The bulbs were securely attached to a piece of hardware cloth 6 inches square. The various roots to be tested were fastened to this wire by means of rubber bands. The bulbs always stood perpendicular to the bottom of the chamber, and the roots were always arranged on the cloth parallel to the bulbs.

Careful tests showed that, while the temperature was uniform at given levels within certain limits, it varied slightly at different levels. Because of this fact, a complete record as to the injury in the lower and in the upper ends of the roots was kept. To further standardize this variation, all of the pieces of material used were cut 4 inches in length. When the

[2] This is a standard apparatus obtainable from the Leeds, Northrup Company, of Philadelphia.

hardware cloth and the bulbs were in position, the roots extended to within one inch of the bottom of the chamber in a regular row.

The difference in temperature on either side of a bulb — that is, horizontally — within a compass of five inches was found to be negligible. However, a number of tests of the temperature in either extreme end of the freezing chamber showed that a maximum difference of one centigrade degree might exist. Accordingly, no roots were tested at these points.

In order to subject all the material to as nearly uniform conditions of freezing as were possible, the killing temperature of a number of different roots was determined at the same time rather than an attempt being made to freeze at once many roots of a single sort. Owing to the variety of roots used, however, it was neither practicable nor desirable to test all of these at any one time. As they naturally divided themselves into groups of more or less tenderness, material of similar resistance was usually frozen together.

While the temperature was being gradually lowered, the inner compartment was kept tightly closed. In no case were any of the roots removed before the minimum degree was reached.

Since several workers have found a distinct influence in the amount of injury resulting from the rapidity of cooling, care was taken to allow a standard rate of fall for all freezings, except as noted to the contrary. This uniform lowering of temperature began at 1.5° C., and reached 0° in fifteen minutes. The fall from this point to the desired degree was at the rate of one degree every twenty-two and one-half minutes. The minimum temperature was always maintained for fifteen minutes. Ordinarily the roots were removed from the chamber and allowed to thaw rapidly.

Russell (1914) and others have noted that the death of a plant from freezing is rarely immediate but may be delayed for several days. Because of this possibility the treated roots were set aside and examined at different intervals. During this time they were kept moist by placing them on a hardware cloth which projected above the surface of the water in an agate pan. The roots and the pan were covered with a bell jar.

An inspection of the roots for injury was usually made within from one to three days after exposure. In most cases when injury occurred, it was apparent by the end of this period. At first microtome sections were prepared and the character of the injury was determined with a low-

power microscope. This was soon found to be unnecessary, since the color changes of the frozen cells, except in the gooseberry and the currant, were rather striking. The affected tissues of the apple became of some shade of brown and appeared water-soaked; in Mazzard cherry, Myrobalan plum, and red raspberry roots, the injured cells were somewhat yellowish; while in the blackberry and the dewberry they often appeared almost black. The early appearance of Rhizopus species and probably other saprophytic fungi on the dead part was also characteristic of injury. In not an instance did the fungus or the discoloration appear in the unfrozen roots left similarly located for comparison.

The roots of all species tested from October 24 to November 18 were collected from the nursery row. All the leaves were present on the plants used in the first determinations and some had not fallen in the latter freezings. The remainder of the material was kept in common storage and removed as needed. With this material the temperature varied somewhat, due to outside changes, but it seldom went below 0° C. and did not rise above 5° until April 1. The plants were stored in normally moist sawdust, and there was little opportunity for them to dry out later as they were placed on the hardware cloth attached to the resistance bulb while in storage and were then immediately frozen.

RESULTS OF THE EXPERIMENTS

RESISTANCE OF APPLE ROOTS TO LOW TEMPERATURE

For all the tests conducted, the diameter of each end and of the center of the root, and the date of freezing, are recorded as possible factors that might influence the kind or the amount of injury. The results of the tests with apple roots are shown in table 1.

Four kinds of seedlings were used: one-year American stocks, grown in this country but from French seed; one-year French seedlings imported from France; two-year French roots which had grown for one year in the nursery here; and one-year stored French seedlings which had been held at approximately 0° C. in cold storage for one year.

One noticeable feature in the apple freezings was the differences in the individual resistance of roots similarly treated and frozen apparently under the same conditions. Unless the temperature is above or below the average freezing point, all gradations of injury may occur.

TABLE 1. EFFECT OF LOW TEMPERATURE ON ROOTS OF APPLE SEEDLINGS

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—7°	October 24 to November 18	American	7 x 6	2	2	....	....	......
			5 x 4	4	3	50	50	50
			4 x 3	7	....	40	40	40
		2-year French	7 x 5	10	10	....	....	......
			5 x 4	8	5	40	40	40
			4 x 3	6	....	60	50	50
—8°		American	5 x 4	1	1	....	....	......
			4 x 3	8	2	40	20	20
			3 x 3	1	....	50	50	50
		2-year French	7 x 5	3	3	....	....	......
			5 x 4	2	2	....	....	......
			4 x 3	13	2	60	60	60
—9°		American	7 x 5	3	1	35	35	35
			6 x 5	2	....	25	25	50
			5 x 4	4	1	90	90	90
		2-year French	7 x 5	2	2	....	....	......
			5 x 4	6	....	75	75	75
			4 x 3	5	5	....	....	......
—9°	December to January	American	9 x 7	5	2	80	35	35
			6 x 6	4	1	50	45	45
			5 x 4	4	....	75	60	60
		2-year French	7 x 5	6	4	5	5	10
			5 x 3	6	2	35	20	20
			4 x 2	6	3	80	65	65
—10°		2-year French	7 x 5	5	3	45	15	15
			5 x 3	14	1	50	50	50
			4 x 3	11	....	60	60	60
—12°		2-year French	8 x 6	2	....	5	5	5
			4 x 3	3	....	100	100	100
—9°	February to March	American	7 x 6	9	6	20	10	10
			5 x 4	9	4	60	60	60
		2-year French	8 x 5	3	3	....	....	......
			3 x 2	3	....	50	50	50

TABLE 1 (*continued*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—10°	February to March (*continued*)	American	7 x 6	12	10	65	10	......
			5 x 4	8	....	50	50	45
			3 x 2	10	....	55	55	50
		2-year French	7 x 5	3	3	....	....	......
			3 x 2	8	1	65	65	65
—11°		American	7 x 6	12	4	60	30	25
			5 x 4	6	2	55	55	55
			3 x 2	30	20	40	40	40
		2-year French	6 x 5	5	5	....	....	......
			3 x 2	20	11	45	45	45
		1-year French	8 x 5	5	....	....	....	......
			3 x 2	8	2	40	10	30
—12°		American	7 x 6	9	1	80	70	70
			5 x 5	11	....	85	85	85
			4 x 3	8	....	75	75	75
			3 x 2	22	....	80	80	80
		2-year French	6 x 5	5	....	75	75	75
			3 x 2	33	....	85	85	85
		1-year French	8 x 6	4	4	....	....	......
			3 x 2	19	5	....	15	15
		1-year French, stored	8 x 5	4	....	100	100	80
			3 x 2	22	7	55	55	55
—12.5°		1-year French	8 x 6	4	1	50	50	50
—13°		American	7 x 6	8	....	90	90	90
			3 x 2	16	2	75	75	75
		1-year French, stored	3 x 2	9	....	85	85	85
—14.5°		American	7 x 6	15	....	80	80	80
			3 x 2	27	....	90	90	90

TABLE 1 (*continued*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—14.5° (*conc.*)	February to March (*concluded*)	1-year French	8 x 7	2	1	100	100	75
			3 x 2	6	....	100	100	100
—9°	March 29 to April 15	1-year French	8 x 6	2	1	....	60	......
			6 x 4	3	3	....	....	......
		American	8 x 6	8	8	....	....	......
			6 x 4	4	2	25	....	......
		1-year French, stored	8 x 6	3	....	100	100	100
—10°		1-year French	8 x 6	4	....	....	....	......
			6 x 4	4	3	100	45	45
			5 x 3	4	....	60	60	60
		American	8 x 6	5	5	....	....	......
		1-year French, stored	8 x 6	5	1	100	100	100
—11°		1-year French	8 x 6	2	2	....	....	......
			3 x 2	6	....	100	100	100
		American	8 x 6	5	1	75	....	......
			6 x 5	4	....	100	100	100
		1-year French, stored	8 x 6	2	....	100	100	100
—12°		1-year French	8 x 6	3	2	100	100	50
			3 x 2	12	....	100	100	100
		American	7 x 5	8	....	100	100	100
		1-year French, stored	8 x 6	3	....	100	100	100

TABLE 1 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—7°	April 16 to May 8	1-year French	8 x 6	2	2	....	....	......
			3 x 2	5	....	50	50	50
		American	8 x 6	7	1	100	100	90
			6 x 4	4	....	....	....	......
		1-year French, stored	7 x 5	2	2	....	....	......
			3 x 2	4	4	....	....	......
—8°		1-year French, stored	7 x 6	4	4	....	....	......
			3 x 2	13	4	80	25	25
		American	8 x 6	4	1	80	25	25
			6 x 4	5	....	90	80	80
		1-year French, stored	8 x 6	2	....	10	....	......
			6 x 5	2	....	90	90	90
—9°		1-year French	8 x 6	2	2	....	....	......
			3 x 2	7	7	....	....	......
		American	8 x 6	6	3	25	....	......
		1-year French, stored	7 x 4	2	2	....	....	......
			3 x 2	4	....	100	100	100
—10°		American	8 x 6	6	....	70	60	60
			6 x 5	6	....	100	100	100

It is a common opinion among some nurserymen that the French-grown apple stocks are hardier than the home-grown seedlings. The results obtained from the freezing of hundreds of roots of each stock indicate that these differences in resistance are negligible. Both stocks are found to show considerable injury from −11° to −11.5° C., and at −12° few of either sort survived. The two-year French roots were grown

under unfavorable conditions in the nursery, and apparently because of this were more easily killed than the one-year stock. The one-year seedlings held in cold storage for one year showed about the same hardiness as the two-year roots.

The observations of Chandler (1913) led him to conclude that the hardiness of the root tissues varies with the season. This is to be expected and the results obtained readily support this theory. The material frozen in October and November shows a marked tenderness compared with roots tested in February and March. The period of maximum resistance seems to end somewhat before the last of March, tho the date would, of course, vary with the conditions affecting after-ripening and possibly also with the variety. From the first of April until these observations ceased, an increasing amount of injury was noted. This range of hardiness indicates a difference in resistance of between three and four centigrade degrees. These seasonal differences obtain, not only in the apple seedlings, but in all the roots reported in this paper.

The influence of the size of the root in withstanding cold seems reasonably well established by the data in table 1 as well as by those in the succeeding tables. The resistance is in direct proportion to the diameter of the root. In practically all cases in which the whole forked roots of the French seedling were employed, the small roots killed first. Similarly, the smaller roots of the American stocks having the same soil depth suffered more quickly and severely than the larger roots.

The results in the apple tests seem to point rather clearly to the relative resistance of the different tissues in these roots. It is seen, in practically all instances in which injury occurs, that the cambium is the first tissue to be killed. This is followed closely by the phloëm, while the cortex seems somewhat hardier than either of the other tissues. Only a few cases are recorded in which the cortex alone was severely injured, tho frequently the three tissues were equally affected. Unless the temperature is especially low for apple roots, or they are especially tender as in the fall and the spring, the cambium, the phloëm, and the cortex are browned without further injury. Occasionally under extreme conditions the xylem and the pith may be killed, in which case they both seem to show about equal resistance. An exposure at –20° C. would ordinarily kill all the cells in the roots of any apple seedlings tested in these experiments, even when they were in a dormant condition.

A number of observations were made on material four inches long, in which two inches of the plant represented the stem above the soil level and two inches represented the root below the surface of the ground. From the results of these freezings some indications were given as to just where the tenderness of the root tissues ended and the well-known hardiness of the stem tissues began. Where injury occurred to the specimen, the region of browning much oftener than otherwise extended from the lower end of the root upward, decreasing abruptly at the crown. This is somewhere near the point of differentiation of root and stem structures. It was indicated from these data that this difference in resistance may have been brought about by a change in cellular structure.

While Chandler (1913) seemed to find that roots deeper down in the soil were tenderer than those near the surface, an examination of his data shows that the deeper roots were also considerably the smaller in diameter. Many observations of roots of equal transverse section and growing at different soil levels were recorded from time to time. From the results of these observations, it was suggested that the size of the root was, perhaps, a greater factor in its resistance than the soil depth at which it grew.

From the foregoing considerations it is rather difficult to assign a fixed temperature at which an apple-seedling root may be partially or completely injured by freezing. Examination of all of the material tested showed that, while severe injury is found at exposures ranging from –7° to –13° C., one French root survived a temperature of –14.5°. However, the majority of the dormant roots were seriously injured in the three outer tissues by a temperature of –12° C.

RESISTANCE OF PEAR ROOTS TO LOW TEMPERATURE

In the work with pear roots the comparative tenderness of two-year French stock (*Pyrus communis*) and one-year Kieffer stock was determined. The two-year roots were given the same field treatment the second year as was given to the two-year French apples previously mentioned. A few one-year French stocks were also available in 1916.

In almost all cases, as shown by the data recorded in table 2, the one-year Kieffer roots proved more resistant than either of the French stocks. At an exposure of –10° C. in the January-March period, the Kieffer roots show a less number and percentage affected than do the two-year French

roots. The temperature of –11° during dormancy was too low for the survival of either species. In the April tests at –8° the Kieffer stock again demonstrates its superiority. When exposed to –9° in April the Kieffer shows only a small amount of injury in the phloëm while the two-year French roots were killed thruout.

TABLE 2. Effect of Low Temperature on Roots of Pear Seedlings

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—7°	October 24 to December 15	2-year French	7 x 6	8	6	20	....	......
			4 x 3	5	....	100	100	100
—8°			8 x 6	10	2	75	75	75
			5 x 3	5	....	100	100	100
—9°			7 x 5	3	1	50	50	50
			5 x 3	6	....	100	100	100
—10°			9 x 8	3	....	60	60	60
			4 x 3	6	....	100	100	100
—9°	January to March	2-year French	8 x 6	5	4	100	100	100
			5 x 3	8	....	100	100	100
—10°			9 x 7	4	1	100	100	100
			5 x 4	13	....	100	100	100
		1-year Kieffer	6 x 6	6	3	60	40	40
—11°		2-year French	9 x 7	5	1	80	85	85
			6 x 4	7	....	85	80	80
		1-year Kieffer	7 x 6	7	....	100	100	100
—12°		2-year French	7 x 6	4	....	100	100	100
		1-year Kieffer	8 x 7	2	....	100	100	100
			7 x 6	2	....	10	45	45
—7°	April 1 to 21	2-year French	8 x 6	2	2	....	....	......
			4 x 3	4	3	50	50	50

TABLE 2 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—7° (*conc.*)	April 1 to 21 (*concluded*)	1-year Kieffer	6 x 6 6 x 3	3 3	3	 25	....	 100
—8°		2-year French	8 x 5	3	....	100	100	100
		1-year Kieffer	6 x 6	9	7	100	100	100
		1-year French	6 x 6 5 x 4 4 x 3	2 12 8	2 4	.... 60 70	.... 60 70	...... 60 70
—9°		2-year French	7 x 5	3	....	100	100	100
		1-year Kieffer	7 x 5	3	....	0	15	0
		1-year French	6 x 4 3 x 2	9 7	....	75 100	75 100	75 100
—10°		2-year French	10 x 6	3	....	100	100	100
		1-year Kieffer	7 x 6	3	....	100	100	100
		1-year French	8 x 5	3	....	100	100	100

The pear roots, like those of the apple, showed individual variations — an increase in hardiness with an increase in diameter, a region at the crown less tender than the root below, little influence due to depth below the soil surface, relative tenderness of the same tissues, and a gradual acquiring of hardiness thru the winter, reaching the maximum in February and March. This seasonal hardiness, however, seems rather more delayed in the pear root than in the apple.

If the resistance of the pear and the apple seedlings is contrasted, it is found that an approximate difference of from one to two degrees generally obtains, and sometimes even a much greater difference. Thus, while in March the apple does not begin to show much injury until a temperature of –11° or –12° C. is reached, –10° or –11° is sufficient to kill most of the tissues, except the xylem and the pith, in both the French and the Kieffer pear stocks.

RESISTANCE OF ELBERTA PEACH ROOTS TO LOW TEMPERATURE

The name *Elberta* as used here refers only to the bearing surface of the tree and has no reference to the origin of the roots. The peach stocks probably were derived from several different varieties; at least, the range of variation presented in table 3 indicates such a possibility.

TABLE 3. EFFECT OF LOW TEMPERATURE ON ROOTS OF ELBERTA PEACH TREES

Temperature (centigrade)	Date of freezing	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots			
					Cambium	Phloëm	Cortex	Pith
–8.5°	February 12 to March 24	12 x 6	2	2	......	......	......	......
		5 x 4	4	......	......	......	15	......
–10°		15 x 8	3	......	100	100	100	100
		10 x 6	6	2	90	90	90	60
		7 x 5	5	......	100	100	100	55
		5 x 4	7	......	65	65	65	45
–11°		15 x 8	1	......	100	100	100	......
		10 x 9	5	......	30	30	35	45
		7 x 5	4	2	......	......	......	100
		5 x 4	7	......	35	35	35	100
–12°		12 x 8	5	......	60	60	60	100
		10 x 6	5	......	40	40	40	100
		7 x 5	3	......	......	......	40	100
		4 x 3	4	......	50	50	50	100
–14.5°		7 x 6	5	1	65	65	65	100
		7 x 5	5	1	25	25	35	100

TABLE 3 (*concluded*)

Temperature (centigrade)	Date of freezing	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots			
					Cambium	Phloëm	Cortex	Pith
—5.5°	March 25 to April 25	7 x 5	7	3	....	25	25	......
—7°		11 x 10	3	2	....	100	100	......
		7 x 5	6	2	20	20	20	......
—8°		12 x 6	2	....	....	10	25	......
		7 x 5	2	1	....	60	60	......
		5 x 4	4	....	100	100	100	100
—9°		10 x 6	3	....	100	....	100	......
—10°		11 x 10	3	....	100	100	100	80
—11°		7 x 5	3	....	100	100	100	75

During the middle of February an exposure at −10° C., included in the February–March period, shows an average injury of 75 per cent in all tissues except the xylem in nineteen out of twenty-one roots. The tests at −11°, which were made on March 1, indicate an average injury of less than 50 per cent. An average injury of from 55 to 60 per cent in all the cells is seen at a temperature of −12°, altho at two and one-half degrees lower two roots out of ten were uninjured.

As a general rule the order of resistance of the various tissues in the peach root seems to be as follows: pith, cortex, phloëm, cambium, xylem. At −18° C. or below, the xylem was usually killed during the hardiest period. In most cases during February and March the pith is the tissue most easily killed, but in April the cambium is the least resistant.

It is not so easy, with the data at hand, to assign an arbitrary limit within which the peach root is injured by freezing. This is because of the great variation in the root tissues. The peach cambium certainly is as hardy as the pear cambium, tho less so than the apple. Regardless of the size of the root, most of the peach material tested showed some injury

at −10° C., and, except in unusual cases, serious injury occurred at −11°. This would then place the hardiness of the peach root very close to that of either pear seedling.

COMPARATIVE RESISTANCE OF MAZZARD AND MAHALEB CHERRY ROOTS TO LOW TEMPERATURE

In the cherry freezing determinations previous to January, 1916, only two-year cherry seedlings were used. Subsequent to that date, only one-year material was tested. A few roots of *Prunus Besseyi* were available in March.

TABLE 4. EFFECT OF LOW TEMPERATURE ON MAZZARD AND MAHALEB CHERRY ROOTS

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	**Number of roots uninjured**	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
−7°	October 24 to December 11	Mahaleb	7 x 3	5	**5**	......	....	......	......	......
			5 x 4	5	**4**	25	....	......	......	......
		Mazzard	8 x 3	2	....	50	50	50	......	......
			7 x 5	2	....	50	50	50	......	......
−8°		Mahaleb	10 x 8	2	**2**	......	....	......	......	......
			9 x 7	3	**1**	25	25	25	......	......
			5 x 4	5	**3**	15	....	......	......	......
			4 x 2	5	....	50	60	60	......	......
		Mazzard	9 x 5	1	**1**	......	....	......	......	......
			5 x 3	4	....	80	80	80	......	......
−9°		Mahaleb	6 x 5	10	**4**	50	....	......	......	......
			5 x 3	2	**1**	50	....	......	......	......
		Mazzard	6 x 5	4	....	80	80	80	......	......
−10°		Mahaleb	10 x 5	2	**1**	......	 50	......	......	......
			5 x 2	2	....	100	100	100	......	......
−12°		Mahaleb	15 x 13	2	....	100	100	100	......	......
−9°	January 1 to March 29	Mahaleb	7 x 5	2	**2**	......	....	......	......	......
		Mazzard	6 x 6	2	**2**	......	....	......	......	......
			5 x 4	3	....	45	45	45	......	......
−10°		Mahaleb	6 x 2	2	**2**	......	....	......	......	......
		Mazzard	7 x 6	2	....	30	30	30	......	......
			4 x 2	2	....	......	....	......	......	......
−11°		Mahaleb	7 x 5	6	**6**	......	....	......	......	......
			4 x 2	2	....	50	50	50	......	......
		Mazzard	8 x 8	6	....	85	85	85	......	......
			5 x 4	4	....	100	100	100	......	......

TABLE 4 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
—11° (*conc.*)	January 1 to March 29 (*concluded*)	Prunus Besseyi	9 x 7	2	....	100	100	100	......	......
			6 x 3	4	....	100	100	100	......	......
—12°		Mahaleb	7 x 6	3	2	10	10	10	......	......
			6 x 3	2	....	100	100	100	......	......
		Mazzard	7 x 6	4	....	100	100	100	......	......
		Prunus Besseyi	7 x 8	2	....	50	....	25	......	......
			7 x 6	2	....	100	....	30	100	......
—15°		Mahaleb	10 x 8	7	....	20	20	20	......	......
			7 x 6	2	1	30	30	30	......	......
		Mazzard	10 x 8	7	....	100	100	100	......	......
		Prunus Besseyi	7 x 7	2	....	100	100	100	......	......
—17°		Mahaleb	8 x 7	2	....	75	75	75	......	......
		Mazzard	8 x 7	2	....	100	100	100	100	......
		Prunus Besseyi	9 x 7	4	....	100	100	100	100	50
—7°	March 30 to April 20	Mahaleb	9 x 4	2	2	......	....	......	......	......
		Mazzard	9 x 8	4	....	100	100	100	......	......
—8°		Mahaleb	8 x 5	4	4	......	....	......	......	......
		Mazzard	12 x 11	2	1	40	40	40	......	......
			8 x 6	2	....	100	100	100	......	......
—9°		Mahaleb	9 x 5	2	2	......	....	......	......	......
			8 x 3	5	4	15	15	15	......	......
		Mazzard	10 x 8	5	....	100	100	100	......	......
			8 x 5	5	....	100	100	100	......	......
—10°		Mahaleb	7 x 6	5	5	......	....	......	......	......
			5 x 2	2	....	40	40	40	......	......
		Mazzard	10 x 9	4	....	100	100	100	......	......
			8 x 8	4	....	100	100	100	100	50
—11°		Mahaleb	8 x 4	2	2	......	....	......	......	......
		Mazzard	8 x 8	3	....	100	100	100	100	......
—12°		Mahaleb	9 x 6	2	....	60	75	75	......	......
			7 x 4	3	....	5	....	10	......	......
		Mazzard	12 x 10	2	....	100	100	100	100	
			8 x 7	4	....	100	100	100	100	100
			7 x 4	3	....	100	100	100	100	100

The most striking fact brought out by the data in table 4 is the uniform tenderness of the Mazzard as compared with the Mahaleb stock. This difference can readily be seen in any comparable instance. It extends thru all stages of maturity. Thus, during November, Mazzard tissue was injured much more severely when exposed to –8° C. than was corresponding Mahaleb stock tested at –9°. In the January–March period a similar difference is noted; the six larger Mazzard stocks given an exposure at –11° show 85 per cent browning in the three outer tissues, while three smaller Mahaleb roots were similarly affected only 10 per cent when exposed at –12°. At –15° the Mahaleb tissue suffers relatively little injury, but the two roots subjected to –17° are mostly killed. In the March–April period the continued resistance of the Mahaleb tissue is striking. On April 15 it is about three or four degrees hardier than the Mazzard, which when exposed to –10° is seriously injured in the pith and the xylem. These results are in accord with the field observations of Craig (1900) and the laboratory studies of Chandler (1913).

The freezing tests with *Prunus Besseyi*, altho this is a plum species, are included in the cherry data since it is frequently used as a cherry stock. These results with *Prunus Besseyi* do not bear out the experience of most writers regarding its exceptional hardiness. During the January–March exposures, it is noted that at –11° C. this variety was injured somewhat more than was the Mazzard. At –12° it was rather more resistant than the Mazzard but the pith in the smaller roots was killed thruout. At –15° and –17° it suffered equally with the Mazzard or worse.

Under field conditions with severe freezing, Craig (1900) found *Prunus Besseyi* much hardier than all other stocks used for cherries. The writer is not prepared to say that the hardiness of this species has been overestimated. His own very limited experience, however, shows it to be inferior in resistance to Mahaleb, and slightly better than Mazzard. Since the writer is not familiar with the *Prunus Besseyi* stock, it is of course possible that the roots tested as recorded above were not of this species. The only evidence that they were correctly named is from the nurseryman who sold them as such.

A small amount of data on *Prunus avium* and *Prunus pennsylvanicum*, not included in table 4, indicate merely that these roots seem to be quite as easily killed by freezing as are Mazzard roots. Since these roots were taken directly from the partly frozen ground in April, they were rather

moist and were probably beginning activity. A larger number of determinations under different conditions might entirely change the tendency just mentioned.

Considering the data on the four cherry stocks, their order of relative hardiness seems about as follows: Mahaleb, *Prunus Besseyi*, *Prunus pennsylvanicum*, Mazzard. If the Mahaleb cherry is compared with the apple, it is seen that the resistance of the former is markedly superior in most cases. In large Mahaleb roots during their hardiest period, little injury is found under –14° C., while at –15° the injury is relatively small. *Prunus Besseyi* did not survive a temperature of –11°. *Prunus pennsylvanicum* succumbed at –10° or –11°, altho the date of freezing may partly account for its tenderness. The Mazzard roots in no instance withstood –11°, but the number of tests run at –10° was insufficient to place this as its minimum. From these results the Mazzard cherry stock does not appear hardier than Kieffer pear stock.

RESISTANCE OF MYROBALAN PLUM ROOTS TO LOW TEMPERATURE

Unfortunately, only one commonly used plum stock was available in this work, aside from the *Prunus Besseyi* roots included in table 4 with the cherry stocks. The number of one-year Myrobalan roots tested was too small to give very conclusive results. However, some indication at least of its comparative hardiness may be gained from table 5. The data in this table place the one-year Myrobalan root in the same group in regard to hardiness as the pear and the Mazzard cherry. The Myrobalan plum does not appear quite so hardy as the Kieffer pear and probably it would prove to be less hardy than a vigorous one-year French pear. The fact that the roots of the latter are normally somewhat larger than the average plum roots, would give still more evidence in favor of the superior hardiness of the pear.

TABLE 5. EFFECT OF LOW TEMPERATURE ON MYROBALAN PLUM ROOTS

Temperature (centigrade)	Date of freezing	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
					Cambium	Phloëm	Cortex
—7°	October 24 to December 20	8 x 7	2	....	50	50	10
		5 x 3	5	....	65	65	65
—8°		5 x 4	3	....	100	100	100
—9°		7 x 5	3	1	100	100	100
		5 x 3	2	....	100	100	100
—10°		9 x 5	2	....	80	80	80
		8 x 7	2	....	65	65	65
—9°	January 1 to March 29	7 x 6	6	....	100	100	100
		5 x 4	11	....	30	30	35
		2 x 1	11	....	40	40	40
—10°		8 x 5	2	....	100	100	100
		5 x 4	9	....	80	80	80
—11°		9 x 7	2	....	75	75	75
		5 x 4	4	....	100	100	100
—8°	April 1 to 8	6 x 5	5	....	80	80	80
		5 x 4	7	....	25	25	60
		3 x 2	13	....	80	80	100

RESISTANCE OF THE ROOTS OF SIX GRAPE VARIETIES TO LOW TEMPERATURE

It is well known that there is a rather wide difference in hardiness in the canes of certain varieties of grapes. Such a variation, tho less important and conspicuous, is found also in grape roots. To determine these differences, six varieties were selected for testing, embracing several species.

According to Hedrick (1908), the varieties used represent the following species: Concord, *Vitis labrusca*; Clinton, *Vitis vulpina* and *Vitis labrusca*, the variety being more characteristic of the former species; Diamond, *Vitis labrusca* and *Vitis vinifera*, the former predominating; Lindley, *Vitis labrusca* and *Vitis vinifera*; Norton, *Vitis aestivalis* and *Vitis labrusca*,

the variety being mostly derived from the former species; Cynthiana, *Vitis aestivalis* and *Vitis labrusca*, the former predominating. All of the roots tested were from healthy, one-year plants. Since none of the roots were large in diameter, a greater number could be tested in a single freezing than is possible with most material; also, the uniformity in size excluded variations due to differences in diameter.

The results given in table 6 show clearly that these varieties readily divide themselves into two classes: one in which the tissues are rather resistant to cold, and another in which the roots are relatively easy to kill by freezing. Clinton, Concord, and Diamond belong in the first group; Cynthiana, Lindley, and Norton fall into the second group.

TABLE 6. EFFECT OF LOW TEMPERATURE ON THE ROOTS OF SIX GRAPE VARIETIES

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
—9°	February 1 to March 17	Lindley	3 x 2	11	**11**	......	......	......	......	......
		Cynthiana	3 x 2	10	**10**	......	......	......	......	......
		Diamond	3 x 2	9	**9**	......	......	......	......	......
		Concord	2 x 2	8	**8**	......	......	......	......	......
—10°		Lindley	3 x 2	10	**10**	......	......	......	......	......
			3 x 1	22	......	60	60	60	......	......
		Cynthiana	4 x 3	10	......	75	75	75	......	......
		Diamond	3 x 1	13	**10**	60	60	60	......	......
		Concord	3 x 2	12	**12**	......	......	......	......	......
		Clinton	3 x 2	15	**15**	......	......	......	......	......
—11°		Lindley	3 x 2	12	**2**	60	40	30	......	......
			3 x 1	18	**1**	100	100	100	......	......
		Cynthiana	3 x 2	20	**5**	55	55	55	......	......
			2 x 1	15	......	100	100	100	5	10
		Norton	3 x 2	23	**3**	60	60	60	......	......
			2 x 1	18	**3**	100	100	100	......	......
		Diamond	3 x 2	21	**17**	35	......	......	......	......
			2 x 1	11	**11**	......	......	......	......	......
		Concord	3 x 2	11	**6**	25	25	25	......	......
			2 x 1	71	**54**	45	45	45	......	......
		Clinton	3 x 2	30	**30**		......	......	......	......
			2 x 1	6	**6**	......	......	......	......	......
—12°		Lindley	3 x 2	25	......	100	100	100	......	10
		Cynthiana	4 x 1	14	......	100	100	100	10	......
		Norton	4 x 1	18	**5**	60	60	60	......	10
		Diamond	3 x 1	15	**12**	20	20	20	......	......
		Concord	3 x 1	15	**13**	5	5	5	......	......
		Clinton	3 x 1	18	**18**	......	......	......	......	......
—13°		Cynthiana	3 x 2	8	......	100	100	100	......	......
		Norton	3 x 2	16	......	100	100	100	......	......
		Diamond	3 x 2	18	**18**	......	......	......	......	......
		Concord	3 x 2	20	**20**	......	......	......	......	......
		Clinton	3 x 2	20	**18**	10	......	......	......	......

TABLE 6 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	**Number of roots uninjured**	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
—14.5°	February 1 to March 17 (*concluded*)	Lindley	3 x 2	18	....	100	100	100	40	50
		Cynthiana	3 x 2	8	....	100	100	100	25	30
		Norton	3 x 2	18	....	100	100	100	40	30
		Diamond	3 x 2	27	**9**	60	50	60	......	......
		Concord	3 x 2	27	**22**	2	....	2	......	......
		Clinton	3 x 2	16	**8**	90	90	90	......	......
—15.5°		Diamond	3 x 2	15	**10**	35	35	35	......	......
		Concord	3 x 2	15	**10**	20	20	20	......	......
		Clinton	3 x 2	15	**10**	35	35	35	......	......
—18°		Diamond	3 x 2	12	....	100	100	100	......	40
		Concord	3 x 2	12	....	100	100	100	......	20
		Clinton	3 x 2	12	....	100	100	100	......	......
—8°	March 21 to April 17	Lindley	3 x 2	17	**12**	20	20	20	......	......
		Cynthiana	3 x 2	8	**6**	20	....	......	......	......
		Norton	3 x 1	8	**5**	......	100	100	......	......
—9°		Lindley	4 x 3	9	**4**	15	15	25	......	......
		Cynthiana	3 x 2	8	**2**	65	65	55	......	......
		Concord	3 x 2	11	**6**	30	....	......	......	......
—10°		Lindley	3 x 2	17	....	100	90	90	10	10
		Cynthiana	3 x 2	18	**5**	55	50	55	......	......
		Concord	3 x 2	8	....	10	10	10	......	......
		Clinton	3 x 2	6	**5**	10	10	10	......	......
—11°		Lindley	3 x 2	30	....	65	65	65	......	......
		Cynthiana	3 x 2	24	**1**	90	90	90	......	25
		Norton	3 x 2	6	....	100	100	100	......	50
		Diamond	3 x 2	8	....	100	100	100	......	......
		Concord	3 x 2	13	**5**	65	65	65	......	......
—12°		Lindley	3 x 2	26	....	100	100	100	90	90
		Cynthiana	3 x 2	12	....	100	100	100	75	50
		Norton	3 x 2	31	....	100	100	100	90	85
		Diamond	3 x 2	18	**3**	100	100	100	......	15
		Concord	3 x 2	23	**5**	100	100	100	50	15
		Clinton	3 x 2	20	**2**	100	100	100	50	50
—14.5°		Lindley	3 x 2	12	....	100	100	100	100	85
		Cynthiana	3 x 2	12	....	100	100	100	100	75
		Norton	3 x 2	12	....	100	100	100	100	60
		Diamond	3 x 2	12	....	100	100	100	100	75
		Clinton	3 x 2	12	....	100	100	100	100	5

Careful comparison of Clinton, Concord, and Diamond during two seasons showed that in 1916 Clinton proved slightly the hardiest, Concord was second, and Diamond was the tenderest of the three. In 1917 Diamond still ranked third, but Clinton and Concord exchanged places. However, the differences in either case were always very small and were probably due to inherent variation. On examination of the determinations made previous to March 17 (table 6), the limits of this hardier group are appar-

ent. Only scattering injury is recorded at –11°, –12°, and –13° C. At an exposure of –14.5°, twenty-two out of twenty-seven Concord roots were uninjured and only a trace of cambium and cortex injury was noted in the remainder. One-half of the Clinton and two-thirds of the Diamond roots were injured more than 50 per cent by the same temperature. At –15.5° an injury of 20 per cent is seen in one-third of the Concord roots and 15 per cent more in the other two varieties. At –18°, however, the cambium, phloëm, and cortex tissues were completely injured in all roots, with some xylem injury in the Diamond and the Concord. By March 21 tenderness began to return, and a few days later these varieties were severely injured by temperatures several degrees higher.

A contrast of the root resistance in the varieties of the second class shows the following order of hardiness: Norton, Lindley, Cynthiana. The variations, however, are so slight that they may be entirely disregarded.

In 1917 Cynthiana was quite as resistant as Norton, as shown by the injury in both at the higher and lower temperatures. Lindley seemed to be a trifle easier to kill than either Cynthiana or Norton in 1916, but here again the differences are slight. The limits of this second group as shown in table 6 lie between –10° and –12° C., the roots usually undergoing considerable injury at –11°. In relative hardiness this places these varieties between the Mazzard cherry and the apple.

The Clinton, Concord, and Diamond roots, even excluding the influence of size, are considerably more resistant than apple roots, and Concord and Clinton seem equal if not superior to the Mahaleb stock.

The results shown on comparing the hardiness of the respective species of grapes are somewhat as would be expected. *Vitis aestivalis*, represented by Norton and Cynthiana, is not adapted to severe cold, and this may account for the fact that its range is limited to the South. The tenderness of Lindley is probably due in part to the influence of *Vitis vinifera*, which, as is well known, will not survive the winter in the latitude of New York State without much protection. Concord and Diamond represent *Vitis labrusca*, the Northern Fox grape, which, while restricted in distribution, is found in Maine. *Vitis vulpina*, represented by Clinton — a variety with extremely resistant roots — has the greatest range of any American species of grape, it having been found in Canada north of Quebec.

RESISTANCE OF BLACKBERRY, DEWBERRY, AND RED RASPBERRY ROOTS TO LOW TEMPERATURE

An attempt was made to test representative varieties of blackberries, dewberries, and red raspberries, in order to determine any varietal or specific differences in the hardiness of their roots. But, since many of the roots either were dead when received or blackened soon afterward, little variation among varieties is recorded. Only one-year plants were used. Since the one-year roots of the black raspberry are so small, and injury to them is difficult to detect, no data are given on this species.

Comparison of the resistance of the blackberry varieties recorded in table 7 shows the Eldorado to be apparently the least affected. The roots of the Early Harvest and the Watt show about equal tenderness.

TABLE 7. EFFECT OF LOW TEMPERATURE ON THE ROOTS OF BLACKBERRY, DEWBERRY, AND RED RASPBERRY

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	**Number of roots uninjured**	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
—9°	March 6 to 20	Eldorado	5 x 4	5	**5**	......	....	......	......	......
		Watt	5 x 4	5	**1**	50	50	50	......	......
		Early	6 x 5	2	**2**	......	....	......	......	......
		Harvest	5 x 4	3	....	45	45	45	......	......
		Lucretia	4 x 3	5	**5**	......	....	......	......	......
		Austin	5 x 4	5	**2**	85	85	85	......	......
—10°		Eldorado	3 x 2	10	**10**	......	....	......	......	......
		Watt	3 x 2	7	....	60	60	60	40	......
		Early Harvest	3 x 2	11	**9**	50	50	50	50	
		Lucretia	3 x 2	10	**9**	25	25	25	......	......
		Austin	3 x 2	10	**9**	25	25	25	......	......
—11°		Eldorado	5 x 4	6	**4**	15	15	15	......	......
		Watt	5 x 4	7	**5**	100	100	100	50	......
		Early Harvest	5 x 4	6	**5**	100	100	100	......	......
		Lucretia	5 x 4	5	**4**	50	50	50	......	......
			3 x 2	8	**3**	100	100	100	......	......
—12°		Eldorado	6 x 5	12	....	100	100	100	20	......
		Watt	6 x 5	10	....	100	100	100	20	
		Early Harvest	5 x 5	5	....	100	100	100	35	......
		Lucretia	5 x 4	8	**1**	75	75	75	......	......
		Cuthbert	4 x 4	6	....	100	100	100	100	......
—7°	March 23 to April 17	Eldorado	6 x 5	2	**1**	......	....	......	10	......
			3 x 2	11	**11**	......	....	......	......	......
		Watt	3 x 2	7	**7**	......	....	......	......	......
		Early Harvest	3 x 2	7	**7**	......	....	......	......	......
		Lucretia	2 x 1	17	**15**	......	....	25	......	......
		Austin	2 x 1	11	**11**	......	....	......	......	......

TABLE 7 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Diameter of roots (millimeters)	Number of roots	**Number of roots uninjured**	Per cent of cells killed in injured roots				
						Cambium	Phloëm	Cortex	Pith	Xylem
—7° (*conc.*)	March 23 to April 17 (*concluded*)	Cuthbert	4 x 3	6	6	......	......	......	......	......
		Perfection	3 x 2	10	......	......	......	......	......	......
		Loudon	4 x 3	5	4	......	......	10	......	......
			3 x 2	4	2	......	......	25	......	......
—8°		Eldorado	7 x 2	4	4	......	......	......	......	......
		Watt	3 x 2	7	7	......	......	......	......	......
		Early Harvest	3 x 2	6	6	......	......	......	......	......
		Lucretia	5 x 5	3	3	......	......	......	......	......
			3 x 2	20	14	50	50	50	......	......
		Cuthbert	7 x 5	3	3	......	......	......	......	......
			3 x 2	3	......	......	......	100	......	......
		Perfection	5 x 3	5	3	......	......	100	......	......
		Loudon	6 x 4	4	4	......	......	......	......	......
			4 x 2	4	......	......	......	50	......	......
—9°		Eldorado	8 x 8	3	1	70	20	20	50	......
			5 x 5	8	......	60	60	60	30	35
		Lucretia	4 x 3	10	9	25	25	25	......	......
			3 x 2	4	2	20	20	20	......	......
		Cuthbert	5 x 5	4	2	100	100	100	......	......
			3 x 2	3	......	......	......	100	......	......
		Perfection	3 x 2	4	3	90	90	90	......	......
—10°		Eldorado	6 x 5	9	1	95	100	95	100	60
		Lucretia	3 x 2	8	2	55	55	55	......	......
		Cuthbert	5 x 4	6	......	100	100	100	......	......
		Perfection	3 x 2	10	......	100	100	100	......	......
—11°		Eldorado	6 x 5	10	......	100	100	100	50	50
			7 x 2	2	......	75	75	75	60	......
		Watt	5 x 4	3	......	100	100	100	100	80
		Lucretia	5 x 4	6	1	90	90	90	75	75
		Cuthbert	5 x 3	9	......	100	100	100	......	......
		Perfection	5 x 4	7	......	100	100	100	......	......
—12°		Eldorado	5 x 4	5	......	100	100	100	100	100

At an exposure of –9° C., three roots out of five of the Austin dewberry were killed while the Lucretia was unhurt. In practically all comparable freezings, the Lucretia seems a trifle hardier than the Eldorado blackberry, but the margin of difference is small.

A comparison of the red raspberry varieties indicates the advantage of the Cuthbert root over the Perfection. The number of Loudon roots tested was not sufficient to permit comparison. Contrast of the relative resistance of Cuthbert as compared with Lucretia suggests the superior hardiness of the latter, while Cuthbert has the approximate killing point of the Eldorado blackberry.

It is seen from the results given in table 7 that none of this Material survived a temperature of –12° C. However, many of the larger roots tested at –11° previous to March 20 were uninjured. Their relative hardiness, therefore, would place these varieties in the group with the Myrobalan plum and the Mazzard cherry.

RESISTANCE OF GOOSEBERRY AND CURRANT ROOTS TO LOW TEMPERATURE

The study of the freezing point of gooseberry and currant roots offered more difficulty than any other determinations undertaken. During the winter of 1915–16 a large amount of currant and gooseberry material was tested; in fact, in nearly every freezing a few roots of these species were included. Upon examination for injury no appreciable change could be observed within the usual time limit. At the end of a still longer period between the testing and the examination, no features were exhibited that the unfrozen roots did not possess. Owing to the pink or reddish pigment found in the cells of the cortex, these cells were examined for injury under the microscope. At –15° C. no discoloration suggesting injury was noted.

It was accordingly decided to repeat the experiment with the gooseberry and the currant roots in a somewhat different way. The varieties were restricted to the Downing gooseberry and the Wilder currant. In this test, whole two-year plants were root-pruned to about four inches and the tops were cut back to four or five branches with three buds left on each. The plants thus treated were then placed in the freezing chamber. At the same time four-inch pieces of root for microscopic examination were tested. After each determination the plants were immediately placed in moist sawdust in common storage, where they were allowed to remain until May 10. On that date they were planted out in the field.

Observations on these plants were taken on June 16, and record was made of the growth that had taken place up to that time. On August 4, the observations were repeated, and it was found that no growth had taken place in any of the specimens recorded as dead in June. These data serve as criteria for the amount of injury that the roots experienced. It is clear that this method is less exact than the previous manner of determining injury by direct observation. It is not possible, for example, to state the size of root affected, or the tissues and the amount of roots

killed, except as these facts are expressed by the relative top growth. Still this test, supplemented by the microscopic observations, should suggest the approximate and comparative resistance of the two species.

TABLE 8. EFFECT OF LOW TEMPERATURE ON GOOSEBERRY AND CURRANT ROOTS (April 3–11, 1917)

Temperature (centigrade)	Serial number	Variety	Number of roots	Depth in soil (inches)	Diameter of roots (millimeters)	Results
—19°	1	Wilder.....	10	6–8	1–6	5 small leaves present; most of stem seemed alive, but growth seriously if not fatally delayed
	2	Wilder.....	9	8–10	2–6	1 small yellow leaf appeared; most of stem tissues brown
	3	Wilder.....	12	6–10	2–6	No leaves present; stem seemed entirely dead thruout
	4	Downing...	13	8–10	1–6	10 or more small green leaves present; stem tissues seemed active
	5	Wilder.....	9	4–8	3–6	Sections examined, 6 mm. and 3 mm. Less than 5 per cent of cortex cells appeared brown
	6	Downing...	8	4 –8	3–6	Sections examined, 5 mm. and 3 mm. Small root seemed the less affected, but 50 per cent of cortex appeared injured in each
—20.5°	7	Downing...	6	4–8	3–6	Sections examined, 6 mm. and 3 mm. No cambium injury; at least 50 per cent of cortex cells appeared injured, with a brownish yellow color
	8	Downing...	9	5–8	1–6	8 small leaves had developed; slightly more injury than in no. 4
	9	Downing...	9	6–8	1–5	No leaves present; buds and stem seemed entirely dead
—18°	10	Wilder.....	8	8	1–6	No leaves present; entire top dead as in no. 9
	11	Wilder.....	7	8	1–6	Same condition of top as in no. 9
	12	Wilder.....	8	8	2–6	Same condition of top as in no. 9
—19°	13	Wilder.....	5	4–8	3–6	Sections examined, 5 mm. and 3 mm. Injury less severe than in no. 7 Downing, but on one side of cortex 50 per cent of cells killed, on the other side 30 per cent injured
—17°	14	Downing...	12	10	1–6	40 or more medium-sized green leaves had developed; more vigorous top than any of preceding
	15	Downing...	15	8	1–6	A few less leaves than in no 14, but all stem tissues active
	16	Downing...	15	8	2–6	Practically the same conditions as in no. 15

TABLE 8 (*concluded*)

Temperature (centigrade)	Serial number	Variety	Number of roots	Depth in soil (inches)	Diameter of roots (millimeters)	Results
—17° (*conc.*)	17	Downing...	9	4–8	1–5	Sections examined, 5 mm. and 3 mm. In small root 25 per cent of cortex cells were of a characteristic yellow color; large root appeared with 35–40 per cent injury
	18	Wilder.....	10	8–10	2–6	Not a leaf present; bud and stem dead thruout
	19	Wilder.....	6	10	1–6	Complete injury to top as in no. 18
	20	Wilder.....	9	6–8	2–5	Sections examined, 5 mm. and 3 mm. 85 per cent of cambium, phloëm, and cortex seemed browned in both large and small root; severest injury thus far observed
—18.5°	21	Downing...	12	10	1–6	15 or more small green leaves present; stem tissues seemed active
	22	Downing...	15	8	1–6	No leaves developed; buds and stem entirely brown
	23	Downing...	9	4–8	2–5	Not more than 10 per cent of injury in cortex, with no browning in cambium or phloëm cells
	24	Wilder.....	10	10	1–5	No leaves present; top still had considerable live tissue
	25	Wilder.....	10	8	1–6	No leaves developed; buds and stem entirely dead
	26	Wilder.....	8	4–8	2–5	Only 5 per cent of cortex cells seemed injured, with no browning in other tissues
—18°	27	Wilder.....	18	4–8	1–6	12 leaves present, ranging in size from 1 to 4 cm. wide
	28	Wilder.....	14	8	2–6	No leaves developed; whole top completely dead
	29	Wilder.....	15	8	2–5	No leaves present; small amount of live cortex and phloëm appeared in one stem
	30	Downing...	7	4–8	2–6	25 or more medium-sized leaves; all stem tissues active
	31	Downing...	11	6–9	1–6	A few less leaves present than in no. 30; otherwise the same
—16.5°	32	Wilder.....	9	4–8	1–5	No leaves developed; top appeared dead thruout
	33	Wilder.....	13	6–12	1–6	No leaves developed; considerable active stem tissue
	34	Downing...	11	4–8	1–6	8 leaves present; all stem tissues seemed alive
	35	Downing...	15	4–8	1–6	12 leaves present; no dead tissue in the top

From an examination of numbers 1, 2, 3, and 4 in table 8, the gooseberry seems slightly hardier than the currant. The microscopic examination of numbers 5 and 6, however, are not in accord with the field test. While the roots sectioned were kept for four days under the bell jar before examination, it is possible that the currant, at least in this case, may offer another instance of delayed death after freezing.

In the next test no currants were included. One Downing survived a temperature of –20.5° C. but, since one was killed completely, this minimum would probably be near the limit of the gooseberry's hardiness at this season. However, microscopic observations showed no more cell injury than in material exposed to –19°.

In numbers 10 to 20, considerable evidence is presented to show a greater resistance in the gooseberry root than in the currant. The microscopic examination also bears this out. Further examination of the data from numbers 27 to 35 gives additional proof of the gooseberry's superior hardiness. But in the last determination the increase in tenderness of the gooseberry is noticeable.

One point especially to be remembered in regard to this table is the date of freezing. On comparing the killing temperature of all of the roots in the other species considered, the relative resistance of the currant and the gooseberry, particularly the latter, is very obvious. These differences represent a range of from five to ten centigrade degrees below the killing temperature of the other roots.

SAP CONCENTRATION OF AMERICAN AND FRENCH APPLE SEEDLINGS AND WILDER CURRANT AS MEASURED BY THE FREEZING-POINT DEPRESSION

It was thought possible that the wide variation in hardiness shown by the roots in the preceding experiments might be due in part to differences in the concentration of the cell sap. Consequently an effort was made to ascertain the sap concentration of the various species. Unfortunately, however, in many cases the sap was found to be very difficult to obtain. In the red raspberry, the dewberry, and the grape, respectively, the sap tissue from the roots of twenty-five plants when expressed yielded less than a cubic centimeter of sap. In other cases sufficient material was not available for this determination.

In the few instances reported in table 9, the roots used for each determination were first entirely killed by freezing. The concentration was determined by means of a Beckmann freezing-point apparatus, and the results, expressed as freezing-point depression, are given in table 9:

TABLE 9. SAP CONCENTRATION IN THE ROOTS OF AMERICAN AND FRENCH APPLE SEEDLINGS AND WILDER CURRANT AS MEASURED BY THE FREEZING-POINT DEPRESSION

Date	Variety	Depression
April 25	American apple roots, upper half	2.487
April 25	American apple roots, lower half	2.214
May 12	Wilder currant roots	2.685
May 12	One-year French apple roots stored one year	2.461
May 12	Two-year French apple roots	1.988

The data in table 9 show a considerable difference in depression between the sap of the one- and the two-year-old French apple roots. Indeed, these differences indicate a wider variation than actually existed. The sap concentration of the two parts of the American apple root may partly explain the fact that the upper half of this root usually suffered less injury than did the lower half at the same temperature. A difference in depression of 0.273 should certainly be of some significance. The root of the Wilder currant proved to have the highest concentration of sap of any of the roots tested. It is indeed, the hardiest of these roots. While this superior sap concentration is not without meaning, it probably does not wholly explain the exceptional resistance of this variety to low temperature.

EFFECT OF RAPID TEMPERATURE FALL ON THE FREEZING OF APPLE ROOTS

Pfeffer (1903:235) stated that "resistant plants withstand rapid and slow cooling equally well, and it is doubtful whether a rapid fall of temperature is more injurious to plants killed by freezing than is gradual cooling." Winkler (1913), however, working with Pfeffer, found that various buds endure a much lower temperature when the fall is very slow.

Chandler (1913), testing many kinds of fruit buds and twigs, found the rate of freezing to be an important factor in the killing temperature.

He observed further that the injury by quick cooling seemed more serious when the rapid fall took place in the early part of the freezing period. The latter observation is in accord with Müller-Thurgau's (1880 and 1886) determinations from which he calculated the size and the time of formation of ice masses in the apple and the potato.

Mix (1916) found that tissue from the trunks of apples killed at a temperature several degrees higher when rapidly frozen than when frozen more slowly.

Some data were procured in this study with a view of determining just how great a difference in injury there would be between roots cooled rapidly and those cooled slowly. An attempt was made also to find out whether the severer injury came during the early or the late period of freezing.

In one freezing the temperature of the air surrounding a large number of roots, all but a few of which were American-grown apple seedlings, was lowered from 1.5° to –4° C. in one hour and forty minutes, and from –4° to –8° in twenty minutes, when the roots were removed. In another freezing the temperature with the same kind of roots was lowered from 1.5° to –4° in twenty minutes, and from –4° to –8° in one hour and twenty-five minutes, when the roots were removed. It is difficult to draw conclusions from but one freezing of each kind, and therefore the data are not included. In the second freezing in which the rapid temperature fall was at the beginning — that is, from 1.5° to –4° C.— the killing was slightly the worse, tho a few French seedlings included were not killed as badly as in the first freezing.

Of course it should be borne in mind that the roots in the second freezing probably reached a lower temperature than did those in the first. It is doubtful whether the roots themselves actually reached the temperature of –8° C. in twenty minutes. The results suggest that there is little difference in the effect on the killing temperature, whether the rapid temperature fall is near the point where freezing begins or nearer the point of the killing temperature. Many more freezings would be necessary, however, before conclusive results could be reached.

Another set of three freezings was made in order to learn the effect of rapid temperature fall on the amount of injury done. In one freezing an attempt was made to approach what would be a normal temperature fall, the temperature falling from 1.5° to –8° C. in three hours and ten minutes.

In the second freezing the temperature fell from 1.5° to –8° in forty-five minutes, when the roots were removed. In the third freezing the temperature fell from 1.5° to –8° in fifteen minutes, and the roots were held at that temperature for one hour. It is of course probable that in the second freezing, in which the roots were removed at once when the temperature of the surrounding air had reached –8° C., the tissue of the roots never reached that temperature. The injury was certainly the least with the slow temperature fall; it was somewhat greater in the second freezing, in which the roots were removed at once; and it was markedly greater in the third freezing, in which, after the temperature had fallen to –8° in fifteen minutes, the roots were held at that temperature for one hour. Thus, with the slow temperature fall, of twelve pieces of American roots seven had no injury, one had 15 per cent of the cambium browned, three had from 30 to 35 per cent of the cambium browned, and one had from 50 to 80 per cent of the cambium browned; in the second freezing, in which the roots were removed immediately after the temperature had reached –8° C. in forty-five minutes, of fourteen pieces of American-grown apple roots five were uninjured, one was very slightly injured, three had from 10 to 20 per cent of the cambium browned, with slight injury to the phloëm and the cortex, one had 25 per cent of injury in these tissues, three had from 50 to 75 per cent of injury, and one was apparently killed thruout; in the case of the third freezing, in which the roots were held at –8° C. for one hour after the surrounding air had dropped to that temperature in fifteen minutes, of nineteen pieces of American-grown apple roots seven showed from 25 to 60 per cent of cambium injury and the remainder showed more injury than that, three being killed practically thruout. Comparing these last two freezings with the slow freezing, it is plain that the rapid temperature fall was the most injurious. In all of these freezings careful records were kept as to the resistance of roots near the surface and of those that had grown deeper in the soil, and roots of the same size showed approximately equal resistance regardless of the soil depth from which they came.

EFFECT OF RATE OF THAWING ON THE FREEZING OF ROOTS

Göppert (1830) concluded, after many experiments, that the rate of thawing had nothing to do with the subsequent injury caused by cold. This view was contrary to the popular belief of his time. Sachs (1860)

stated that "the same tissue which, after exposure to freezing temperature, with slower thawing remained alive unhurt, becomes disorganized when with similar freezing it is thawed rapidly." [3] Müller-Thurgau (1886) pointed out that Sachs' method of placing his tissues in cold water to thaw them was really a case of rapid thawing, since a layer of ice formed about the tissues, thus releasing considerable heat. Müller-Thurgau, using many plants and plant parts, found that the ripe fruits of the pear and the apple, and the leaves of *Agave americana* L., were injured somewhat less when slow thawing was practiced. Molisch (1897) confirmed these results of Müller-Thurgau. Chandler (1913), in his experiments, also found that when the temperature did not go too low, slow thawing reduced the injury to ripe apple and pear fruits and to lettuce leaves; the rate of thawing did not influence the amount of injury to the many other tissues studied.

In this work several experiments were conducted to determine the influence of slow and of rapid thawing on most of the root species used. After being lowered to the killing temperature the material was divided into four comparable lots. It was then thawed at the following temperatures: slightly below freezing but gradually rising; at 0° C.; at 8° C. in the basement storage; and at 22° C. in the laboratory. After a number of hours all the lots were placed under a bell jar at room temperature. Slight differences were noted, but these were confined to very narrow limits and seemed to result from an inherent tendency to vary rather than to be due to any particular set of thawing conditions. When summarized the variations practically canceled themselves and no specific effect could be attributed to the rate of thawing.

INJURY TO APPLE ROOTS WHEN FROZEN IN SOIL, IN WATER, AND IN PARAFFIN

Some determinations were made in which American-grown apple roots were placed in the freezing chamber and completely surrounded by a garden loam soil. In one case the soil was well dried by exposure to warm air. In another case enough water was added to the loam to make it rather muddy. A third soil contained a normal amount of moisture. Twenty-five roots were used in each treatment, and, except in the case of the muddy soil, an effort was made to pack the earth about the roots. In a fourth determination water was substituted for the soil. The water

[3] Translation from the original German.

came well above the top of the material. When the thermometer and the roots were removed after the freezing period, the water was frozen into a solid block of ice about them.

The conditions of these determinations seem too artificial to justify the presentation of tables, but the results may be briefly stated. On comparing the influence of the different soils with a normal air determination, it was found that the roots frozen in air-dried loam were very nearly as resistant to cold as were those frozen in the air. The roots treated in muddy and normal soil seemed slightly easier to injure than those tested in the air or in the air-dried loam. However, these differences were hardly large enough to be dependable, especially when the natural tendency of the species to vary is considered. The material surrounded by water manifested no constant behavior different from that of the other roots.

Since it was believed that the freezing might not be uniform in such a large volume of water, and that severer injury might occur in certain areas of the tissue than in other areas due to the presence of air pockets, another test was made some weeks later. One resistance thermometer was placed in a graduated cylinder of 100 cubic centimeters capacity; a second was placed in water in a large test tube $1\frac{1}{2}$ by 5 inches in size; and a third was exposed to the air in the chamber. Pieces of apple root were placed in large test tubes with and without water. While a large quantity of salt and ice was being used, the readings given in table 10 were recorded. It is evident from this table that low temperature can be temporarily excluded by appropriate quantities of water. After a certain period of time, however, such protection becomes ineffective. The length of time of such insulation seems to vary with the volume of water used.

On examining another large test tube taken from the freezing chamber, in which were placed three medium-sized apple roots, it was noticed that some of the water in the tube was unfrozen. It seems significant also that when the roots were examined two days later, not a cell appeared to be injured, while the cambium, the phloëm, and the cortex tissues of three similar roots placed in the air were entirely dead. The water in the graduated cylinder in which a thermometer was placed was completely frozen.

From these facts the effect of the water seems to be due to the unfrozen water. When the entire mass becomes ice, it readily conducts the heat out of the interior.

TABLE 10. INFLUENCE OF AIR AND WATER IN LOWERING THE TEMPERATURE AROUND RESISTANCE THERMOMETERS

(August 4, 1917)

Hour	Temperature (centigrade)		
	Thermometer in graduated cylinder	Thermometer in large test tube	Thermometer in air
3.00	11°	13°	15°
3.20	4.5°	6°	8°
3.30	0°	4.5°	6.5°
3.45	0°	1°	3°
4.00	0°	0°	—0.5°
4.10	—0.5°	—0.5°	—5.5°
4.20	—0.5°	—0.5°	—9.5°
4.30	—0.5°	—0.5°	—10.5°
4.45	—0.5°	—0.5°	—11°
5.00	—0.5°	—0.5°	—11.5°
5.15	—1°	—0.5°	—11.5°
5.30	—2°	—0.5°	—12°
5.45	—7°	—1°	—12°
6.00	—11.5°	—3°	—12°
6.15	—12°	—8°	—12°

A rather extensive series of seventy-one tests was conducted, to determine whether water or paraffin might be possible factors in influencing the amount of injury. The method and results of these tests were as follows:

Apple roots were placed in ordinary test tubes, which were sealed and in their turn put into larger test tubes, and the surrounding space was filled with water, paraffin, or air. Other apple roots were completely coated with melted paraffin and frozen in the usual way, while still others were immersed and frozen in test tubes containing water. All the lots were given an exposure of from –9° to –12° C.

In most cases in which water surrounded the tissue but was not in direct contact with it, some protection from freezing was afforded as compared with material lacking such treatment. As previously noted, the amount of protection seemed directly proportional to the volume of water used. In the case in which the roots were immediately surrounded by water, the protective influence was less pronounced. This may have been due

in part to an increased moisture content of the tissue brought about by several hours of exposure in the water.

Among the roots used in these tests, thirty-six were covered with paraffin and were tested at different temperatures. Of these roots, twenty-five suffered considerably more injury in the three outer tissues than did the corresponding checks, eight seemed to be injured somewhat less than the normal, and three showed injury similar to that in the untreated roots. The removal of the paraffin immediately after the exposure seemed inconsequential.

The cause for this behavior is not readily apparent, unless, perhaps, it may be associated with the phenomenon of supercooling. According to this hypothesis, the coating of paraffin might have functioned to delay ice formation in the tissue by preventing normal inoculation from the surface crystals, thus prolonging the supercooling period. The surrounding air temperature constantly being lowered, more serious damage might have resulted from rapid freezing once ice crystallization began.

INFLUENCE OF THE SCION ON THE HARDINESS OF ONE-YEAR ROOTS OF THE STOCK

In February, 1916, 640 piece-root apple grafts were made, the varieties Tompkins King, Baldwin, Oldenburg, and McIntosh being used as scion wood. These varieties were selected for the scions because of the well-known difference in the hardiness of their twigs. The stocks were taken from long-rooted American seedlings. Each stock was cut into four equal parts, from three to four inches in length. Since the lower pieces of a seedling are smaller than the crown cut, each variety was grafted on each of the four cuts, in order to exclude any variation from this source. This gave sixteen possibilities, each represented by forty plants. The column in table 11 headed "Section of stock" indicates the cut of the stock used; for example, section 1 is the crown cut, section 2 is the first cut below the crown, and so on.

This material was planted out rather early and was given average care thru the summer. The roots were dug after the leaves had fallen, and were placed in common storage until tested. Only the roots that had developed in 1916 from the parent stock were used. They were rather abundant at the lower callus, and were generally from two to three millimeters in diameter. Other roots of the American and French apples were tested from time to time for comparison.

TABLE 11. Influence of the Scion on the Hardiness of One-Year Roots of the Stock

Temperature (centigrade)	Date of freezing	Variety	Section of stock	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
							Cambium	Phloëm	Cortex
—10°	February 21 to 24	McIntosh	1	3 x 3	5	5	......	....	......
			4	3 x 2	5	5	15	....	......
		Oldenburg	3	3 x 2	5	4	......	....	......
			4	4 x 3	5	5	......	....	......
			4	3 x 2	8	8	......	....	......
		Baldwin	1	3 x 3	5	5	......	....	......
			4	3 x 3	5	5	......	....	......
		Tompkins King	4	3 x 3	8	7	50	50	50
			1	3 x 2	5	5	......	....	......
		American	....	3 x 3	4	4	......	....	......
				3 x 2	3	2	......	15	15
		French	....	3 x 2	4	4	......	....	......
—11°	February 17	McIntosh	2	4 x 3	5	5	......	....	......
			3	4 x 3	5	5	......	....	......
			3	3 x 2	4	4	......	....	......
		Oldenburg	2	4 x 3	5	5	......	....	......
			3	3 x 2	10	10	......	....	......
		Baldwin	2	4 x 3	6	4	15	15	15
			3	4 x 3	3	3	......	....	......
			3	3 x 2	12	11	15	15	15
	February 21	McIntosh	2	3 x 2	13	10	25	....	......
		Oldenburg	1	3 x 2	7	5	25	....	......
			2	3 x 2	8	4	30	....	......
		Baldwin	1	3 x 2	13	13	......	....	......
			2	3 x 2	8	5	25	....	......
		Tompkins King	1	3 x 2	8	6	50	25	25
			2	3 x 2	10	....	15	15	15
		American	....	4 x 3	6	6	......	....	......
		French	....	3 x 2	4	4	......	....	......

TABLE 11 (*continued*)

Temperature (centigrade)	Date of freezing	Variety	Section of stock	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
							Cambium	Phloëm	Cortex
—11° (*conc.*)	March 3	American	....	3 x 2	6	4	20	20	20
		French	....	3 x 2	6	4	20	20	20
—11.5°	February 28	McIntosh	1 4	3 x 2 3 x 2	5 6	5 6	....	....	....
		Oldenburg	3	3 x 2	5	....	50	50	50
		Baldwin	3 1	3 x 2 3 x 2	5 3	1 3	50	50	50 ......
		Tompkins King	2	3 x 3	5	2	40	40	40
		American	....	3 x 2	5	1	50	50	50
		French	....	3 x 2	5	....	70	70	70
—12°	February 17	McIntosh	1 4	3 x 2 3 x 2	5 6	....	100 100	100 100	100 90
		Oldenburg	3 4	3 x 2 3 x 2	6 7	....	60 70	60 70	60 70
		Baldwin	1 4	3 x 2 3 x 2	6 6	....	70 90	70 90	70 90
		Tompkins King	1 3	3 x 2 3 x 2	5 6	....	75 60	75 60	75 60
		American	....	4 x 3 3 x 2	2 5	....	75 80	75 80	75 80
		French	....	4 x 3 3 x 2	2 5	....	90 100	90 100	90 100
	February 26	McIntosh	2 3	4 x 3 4 x 3	5 5	....	60 80	60 80	60 80
		Oldenburg	2	4 x 3	6	3	20	20	20
		Baldwin	2 3	4 x 3 4 x 3	5 5	....	100 85	100 85	100 85

TABLE 11 (*concluded*)

Temperature (centigrade)	Date of freezing	Variety	Section of stock	Diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
							Cambium	Phloëm	Cortex
—12° (*conc.*)	February 26 (*concluded*)	Tompkins King	2	4 x 3	5	....	80	80	80
			3	4 x 3	5	....	45	45	45
		American	....	4 x 3	5	....	70	70	70
		French	....	4 x 3	4	....	100	100	100
	March 1 to 3	McIntosh	1	3 x 2	5	....	100	100	100
			2	3 x 2	10	....	60	60	60
			3	3 x 2	5	....	100	100	100
		Oldenburg	1–4	3 x 2	12	2	55	55	55
			2	3 x 2	5	....	80	80	80
			3	3 x 2	7	1	70	70	70
		Baldwin	1	3 x 2	5	....	70	70	70
			3	3 x 2	3	....	85	85	85
			3–4	3 x 2	11	1	70	70	70
		Tompkins King	1–3	3 x 2	11	....	90	90	90
			2	3 x 2	6	....	90	90	90
			3	3 x 2	6	....	70	70	70
		American	....	3 x 2	18	....	70	70	70
		French	....	3 x 2	14	....	70	70	70

The results shown in table 11 require but little comment. At a temperature of −10° C., as was expected, only a negligible amount of injury occurred in any roots. Likewise at −11° most of the root tissues escaped severe browning. An exposure to −12°, however, resulted in serious injury in practically all the roots tested. The temperature of −11.5° suggests a point below which most of the roots are killed, and above which little or no injury takes place in any variety.

The above observations are limited in extent and might not apply to other conditions. However, an analysis of these particular data seems to indicate strongly, not only that the size of the section of root used for the stock has no influence on the freezing point of the new roots, but also

that there are no constant nor considerable differences in hardiness of the roots developed from any of the four different varieties. It is shown further that there is no significant variation in the hardiness of the grafted and the seedling stock.

EFFECT OF SUGAR SOLUTIONS, WATER, AND DRYING OUT, ON THE RESISTANCE OF APPLE ROOTS TO FREEZING

Since a number of investigators have found that certain solutions have various influences on plant tissue with reference to freezing resistance, data were procured to ascertain whether or not similar effects could be observed in the roots. Before consideration of table 12, containing these data, it seems well to briefly mention some of the results reported regarding the influence of moisture content and the concentration of cell sap on the freezing to death of plant tissue.

It is well known that air-dried seeds can resist a very low temperature, but if allowed to absorb water they are frozen rather easily. Müller-Thurgau (1880) found that succulent tissue has a higher freezing point than material with a lower moisture content. Shutt (1903), Selby (1908), Shaw (1911), and Beach and Allen (1915) seemed to find that apple twigs are tender in proportion to the higher moisture content. Mix (1916), on the contrary, reported that tissue from the trunk of apple trees soaked in distilled water for an hour and then frozen was not injured more than normal untreated material.

Bartetzko (1910) found that Aspergillus, Penicillium, and other fungi grown in nutrient solutions of varying concentration, increased their resistance to freezing in proportion to the increase in the osmotic strength of the solution. Ohlweiler (1912) observed that in species of Magnolia in which the cell structure of the leaves was essentially the same, the concentration of sap was an indication of the relative hardiness of the species. Chandler (1913:181) stated, in summarizing his experience in connection with the relation of sap concentration to hardiness, " In case of plants not in a resting condition, a large amount of dissolved material either in the sap within the cell or in a solution surrounding the cell, will protect the cell from injury due to low temperature, to some extent at least." Chandler noted also that apple roots kept in water for eighteen hours were more severely injured than similar material dried in the air for the same period.

Maximow (1914) studied at length the influence of several organic and mineral solutions on the protection of red cabbage and tradescantia cells from cold. He found marked protection from these compounds, except when the solution was of a toxic nature or when it precipitated its solutes at a temperature near the freezing point of the cell sap. Not all of the increased cold resistance, however, was explained by the differences in the depression of the freezing point of the sap.

In these observations (table 12) the concentration of the cane sugar solutions to which the apple roots were exposed varied from 0.1 gram to 3 grams molecular. The length of exposure ranged from twenty minutes to ninety-six hours. Similar treatment was given using tap water instead of a sugar solution. In no cases were the roots frozen in the solutions, as in Maximow's (1914) experiments, and the free surface moisture was always removed. The roots were allowed to dry out at storage or laboratory temperature for from fourteen to sixty-eight hours. In a few instances both the drying-out and the solution treatment were given the same root.

TABLE 12. Effect of Various Previous Treatments on the Freezing to Death of American Apple Roots

Temperature (centigrade)	Date of freezing	Previous treatment	Average diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots		
						Cambium	Phloëm	Cortex
—8°	April 28	Untreated	7 x 6	4	....	25	10	10
		18 hours at 22° in laboratory	7 x 7	7	7	....	....	......
		18 hours in tap water	8 x 7	3	....	50	40	......
		Same treatment	6 x 6	2	....	70	....	......
		18 hours in 0.1 gram cane sugar solution	7 x 6	7	....	55	20	......
		18 hours in 0.05 gram salt solution	8 x 6	3	1	15	10	......
—9°	May 1 to 2	Untreated	7 x 6	16	5	60	20	15
		18 hours at 8° in storeroom	7 x 7	2	1	40	....	......
		44 hours as above	7 x 6	4	3	10	10	......
		44 hours at 22° in laboratory	8 x 6	7	6	10	10	......
		68 hours as above	6 x 5	6	5	65	65	65
		44 hours in tap water	7 x 7	4	....	100	100	100
		68 hours as above	7 x 6	4	....	100	100	100
		68 hours in 0.1 gram cane sugar solution	7 x 6	4	....	100	100	100
		44 hours in 0.2 gram cane sugar solution	8 x 7	4	....	100	100	100
		68 hours as above	7 x 7	6	....	80	70	60
		44 hours in 0.1 gram salt solution	8 x 7	4	1	70	35	5
		68 hours as above	8 x 7	4	....	100	90	80

TABLE 12 (*concluded*)

Temperature (centigrade)	Date of freezing	Previous treatment	Average diameter of roots (millimeters)	Number of roots	Number of roots uninjured	Per cent of cells killed in injured roots: Cambium	Phloëm	Cortex
—10°	May 5 to 10	Untreated	7 x 6	23	5	65	30	20
		48 hours at 8° in storeroom	7 x 6	5	3	10	....	......
		48 hours at 22° in laboratory	7 x 7	2	2	....	....	......
		24 hours in tap water	7 x 7	2	....	100	100	100
		48 hours as above	7 x 6	8	....	90	90	85
		24 hours in 0.5 gram cane sugar solution	7 x 6	2	....	100	100	100
		48 hours as above	7 x 7	4	....	100	100	100
		72 hours in 0.5 gram cane sugar solution; 16 hours at 22° in laboratory	6 x 5	3	1	65	50	50
		20 minutes in 1 gram cane sugar solution	7 x 7	2	2	....	....	......
		24 hours as above	7 x 6	2	....	100	100	100
		48 hours as above	7 x 7	4	....	75	75	75
		72 hours as above	7 x 7	4	....	80	80	80
		96 hours as above	6 x 5	5	....	100	100	100
		72 hours in 1 gram cane sugar solution; 16 hours at 22° in laboratory	6 x 5	5	1	75	60	......
		20 minutes in 2 grams cane sugar solution	7 x 7	2	2	....	....	......
		24 hours as above	7 x 6	4	....	100	100	100
		48 hours as above	7 x 7	4	....	75	75	75
		72 hours as above	6 x 5	2	....	100	100	100
		76 hours as above	9 x 8	1	1	....	....	......
		72 hours in 2 grams cane sugar solution; 16 hours at 22° in laboratory	7 x 6	5	1	90	55	50
		20 minutes in 3 grams cane sugar solution	7 x 7	2	....	100	100	100
		48 hours as above	7 x 7	7	....	100	100	90
		72 hours as above	6 x 5	2	....	100	100	100
		72 hours as above	9 x 8	4	....	100	45	30
		72 hours in 3 grams cane sugar solution; 16 hours at 22° in laboratory	6 x 5	2	....	100	100	100
		96 hours at 22° in laboratory; no injury at −10°; then 48 hours in tap water	8 x 7	2	....	100	100	100

It is readily seen, in essentially all cases in table 12, that the roots kept in cane sugar and salt solutions longer than twenty minutes were injured more than the untreated tissue and about the same as the roots placed in water. On the other hand, roots dried in the air at 8° and 22° C. exhibited less killing than the normal tissue. These conclusions seem true regardless of the freezing temperature used, the time exposure above eighteen hours, or the concentration of the solution employed. The few roots exposed for twenty minutes in sugar solution did not decrease in resistance. More

examples are necessary, however, before these data can be considered dependable.

An interesting fact brought out in this connection is the effect of drying after exposure to a sugar solution. While the roots scarcely recovered normal hardiness in most instances, the percentage of injury was somewhat lessened except when small roots were employed. In the last case shown in table 12, two roots exposed to −10° C. without injury were killed thruout after remaining in tap water for forty-eight hours.

Unfortunately, at the time of this study not enough material was available to determine the freezing-point depression of the sap of the roots kept in sugar solutions. If the sap concentration was increased by such treatment, another factor, or other factors, inhibited its action in lowering the freezing point of the tissue.

According to table 9 (page 643) the depression of the American-grown apple root would indicate a concentration of about 1.33 gram molecular. Since the concentration of the sugar solutions ran as high as 3 grams molecular, either plasmolysis or an increase in the concentration of cell sap would be expected. To determine this point, sections of roots exposed to the various concentrations used in the experiment just described were examined under the microsope. In all cases the cells appeared normally turgid.

The cause of the severer injury to cells of higher moisture content, while often observed, is also rather obscure. It seems, however, that if both the moist and the dry tissues possessed the same initial concentration, at an air temperature of −9° or −10° C. both should possess the same amount of water in the cells, regardless of the injury. Indeed, both have given up the identical amount of water at −10° C., the dry root having lost its water thru evaporation and ice formation, the moist root thru ice formation only. This reasoning suggests that the greater injury in the moist cells may be due to a larger ice mass formed in them. It suggests further that causes other than dehydration must account for the phenomenon of freezing to death of plant tissue.

SUMMARY

There is little difference in hardiness of the roots between American and French apple seedlings. Normal one-year roots are hardier than one-year stocks held one year in cold storage or grown in the field a second year.

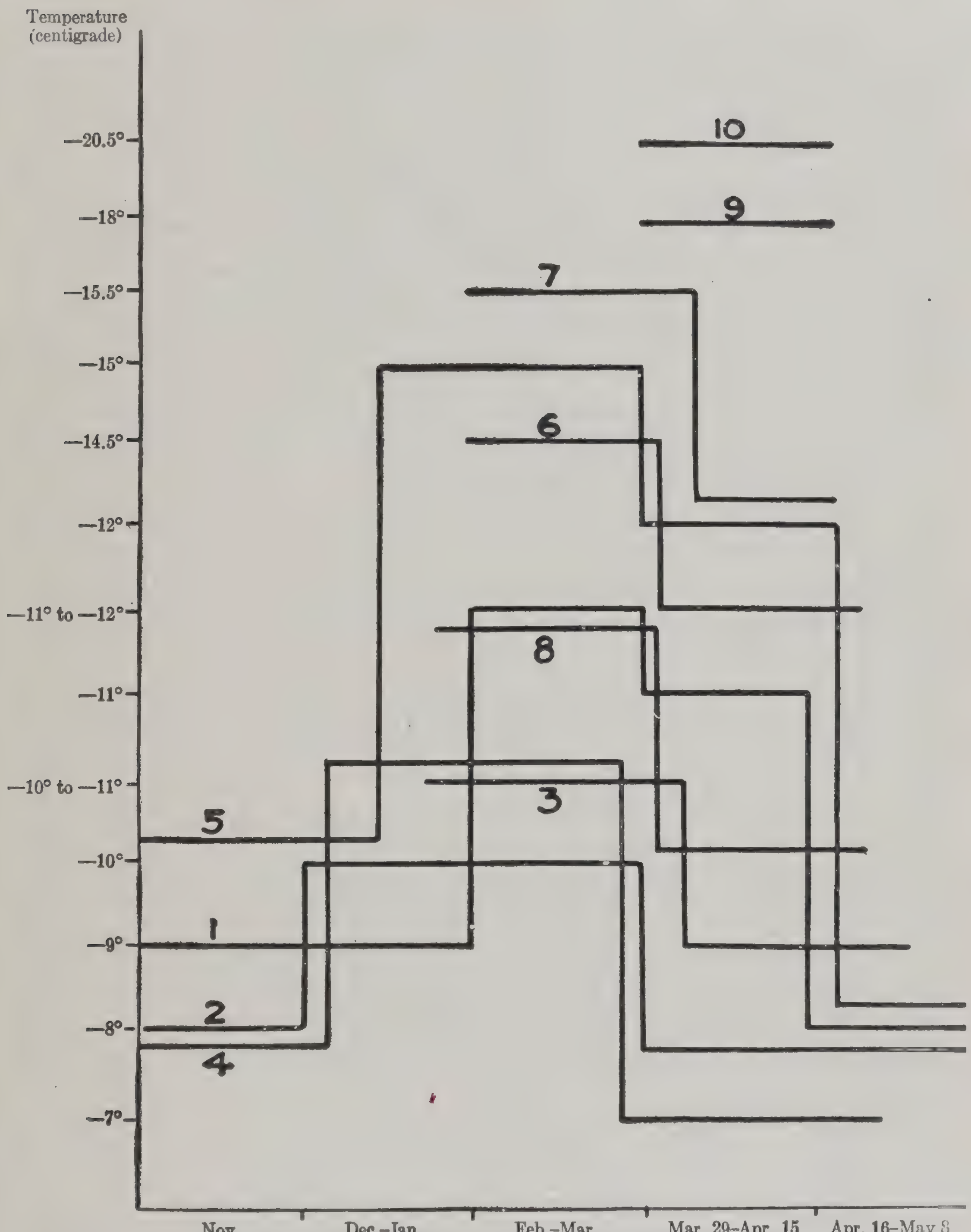

FIG. 164. SEASONAL HARDINESS OF FRUIT ROOTS

1, Apple (French "crab"), and grape (Lindley, Norton, and Cynthiana). 2, Pear (French) and plum (Myrobalan). 3, Peach. 4, Cherry (Mazzard). 5, Cherry (Mahaleb). 6, Grape (Diamond). 7, Grape Clinton and Concord). 8, Raspberry, blackberry, and dewberry. 9, Currant. 10 Gooseberry

The state of maturity and the diameter of the roots were the important factors in determining the resistance to freezing of all species tested in these experiments.

The French pear stock seems more tender than the Kieffer stock. Both roots are less resistant to freezing than is the apple.

Peach roots on which the variety Elberta had been budded proved less hardy than the apple and about equal to the Kieffer pear.

The order of hardiness of the four cherry stocks tested is as follows: Mahaleb, *Prunus Besseyi*, *Prunus pennsylvanicum*, Mazzard. The Mahaleb stock is considerably superior to the apple, while the Mazzard is about equal to the French pear.

Myrobalan plum roots are quite as easily killed by low temperature as are the French pear and the Mazzard cherry.

In the six varieties of grapes studied, the roots of the Clinton and the Concord are as hardy as the root of the Mahaleb cherry. The Diamond is slightly less hardy. The roots of the varieties Lindley, Norton, and Cynthiana are more resistant than the root of the Mazzard cherry but less resistant than the apple root.

No significant differences are seen between the hardiness of the blackberry root and that of the red raspberry root. The Lucretia dewberry, however, is slightly less tender than either, and is about equal to the apple stock.

Roots of the Downing gooseberry are more resistant to freezing than are Wilder currant roots. The roots of the gooseberry and the currant seem much hardier than any other roots examined.

The freezing-point depression of the Wilder currant sap is greater than that of the apple sap. Sap from the upper half of American-grown apple roots is of a higher concentration than that from the lower half of the same roots. The upper half of the root is also somewhat more resistant to cold.

A rapid fall in temperature is shown to increase the freezing injury in apple roots.

The placing of soils of different moisture content in the freezing chamber around the roots causes no appreciable difference in the amount of injury.

A majority of roots entirely covered with melted paraffin killed more severely than did similar untreated roots.

Water, when placed in the same test tube with the root tissue or when placed around it in another container, often provides protection against a low temperature, until all the water is frozen.

The hardiness of the scion does not seem to affect the resistance of the one-year roots of the apple stock.

Roots placed in sugar solutions varying in concentration from 0.1 gram to 3 grams molecular, are injured more easily than are normal roots. Roots allowed to absorb moisture for several hours are similarly injured.

In nearly all cases in which the material was allowed to dry, its resistance was increased.

The difference in the response to cold of the moist tissue and the dry tissue may be due to the smaller ice mass formed in the dry root.

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FREEZING INJURY IN ROOTS OF SOME FRUIT SPECIES

1, Apple. 2, European pear; 3, Kieffer pear. 4, Elberta peach

FREEZING INJURY IN ROOTS OF SOME FRUIT SPECIES

1, Morello cherry; 2, Mahaleb cherry. 3, Myrobalan plum. 4, Concord grape. 5, Red raspberry. 6, Gooseberry, uninjured after fifteen hours exposure at –22° C.

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A MODIFIED BABCOCK METHOD FOR DETERMINING FAT IN BUTTER

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CONTENTS

A MODIFIED BABCOCK METHOD FOR DETERMINING FAT IN BUTTER

A MODIFIED BABCOCK METHOD FOR DETERMINING FAT IN BUTTER[1]

Nelson W. Hepburn

The problem of devising a short method for determining the fat content of butter was formerly a subject of academic rather than practical interest. Within recent years, however, there has been a notable development within commercial systems which has brought with it new demands. The fundamentals necessary to good instruction for the improvement of manufacturing systems have become more fully understood. Increased commercial competition has developed a higher regard for a more accurate accounting of the product as it passes thru the plant, and commercial institutions have insisted on a more far-reaching legal supervision over the composition of their products.

One serious difficulty in meeting these demands with respect to the manufacture of butter has been the lack of a method for quickly and accurately determining the fat content of this product. The purpose of the investigation herein discussed was to develop such a method. Since the Babcock test apparatus is regularly a part of present-day commercial equipment, it seemed that some modification of this method would naturally be the most acceptable. Other modification have been suggested for this purpose at various times (Wiley 1899, Wright 1904, Farrington and Woll 1914, Van Slyke 1916),[2] but no method has appeared which satisfactorily meets the commercial needs.

METHODS OF THE PRESENT INVESTIGATION

One suggested modification of the Babcock test involved the use of an ordinary Babcock cream bottle with a fractional sample of butter. Early in the history of the hand-separator cream industry, samples of cream rich in fat were frequently tested by using a 9-gram sample in an 18-gram bottle. This procedure was often accompanied by a relatively high degree

[1] Also presented to the Faculty of the Graduate School of Cornell University, June, 1918, as a major thesis in partial fulfillment of the requirements for the degree of doctor of philosophy.

[2] Dates in parenthesis refer to *References cited*, page 690.

of error, due to the fact that when 9 grams of cream are weighed into an 18-gram bottle any errors in weighing or reading are multiplied by the factor 2. If these errors happen to fall in the same direction, the final results may be far from accurate. This criticism is even more applicable in the testing of butter than in the testing of cream, since butter is more difficult to manipulate than is cream.

In this investigation, preliminary to the undertaking of the development of a special method a number of samples of butter were tested by the ordinary Babcock method, the cream bottle being used with a fractional sample. This method of manipulation was as follows: Half samples (9 grams) of butter were used in an 18-gram, 40-per-cent cream bottle. A 9-gram sample was introduced into the bottle, 9 cubic centimeters of warm water was added, and this was followed by 17.5 cubic centimeters of sulfuric acid. After thoroly mixing the water, the fat, and the acid, enough more water was introduced to bring the fat up to the base of the neck in the bottle. Tests were then centrifuged at the ordinary rate of speed for a period of five, and then of four, minutes. The samples were then removed from the tester, set in a water bath, and tempered at from 125° to 130° F. Glymol (Hunziker and others, 1910) was added to remove the meniscus in reading. The average readings were multiplied by 2 to give the percentage of fat in the butter. Some of the results of this preliminary study are given in table 1:

TABLE 1. RESULTS OF TESTS MADE WITH AN 18-GRAM, 40-PER-CENT CREAM BOTTLE

Reading			Calculated percentage of fat	Chemical analysis
Minimum	Maximum	Average		
42.25	42.56	42.40	84.74	84.09
42.75	42.75	42.75	85.50	83.99
41.75	42.00	41.87	83.74	82.74
41.25	41.50	41.37	82.74	83.85
42.50	42.50	42.50	85.00	84.21
41.25	41.50	41.37	82.74	83.85
42.00	42.00	42.00	84.00	82.74
41.75	42.00	41.87	83.74	82.76
42.14	42.50	42.32	84.74	83.99
41.50	42.25	41.87	83.74	84.38

The results given in table 1 are typical of those obtained in testing about one hundred samples of butter, using the fractional sample in the ordinary cream bottle. The relatively high degree of error observed in some of these cases is obviously due to the fact that an exact reading is difficult in this type of bottle and in the final results any errors in manipulation have been doubled. It is evident, then, that uniformly accurate results are not obtained by this method. It therefore seemed advisable to construct a type of bottle in which the final results would be obtained by direct weighing and direct reading.

The problem of developing a test bottle for this purpose was bounded by the following requirements: (1) The bottle must be of such dimensions that it would fit the ordinary Babcock centrifuge; (2) it must be so constructed that the graduated part of the neck would hold all the fat for a given weight of sample; (3) the relation of the diameter of the neck to its length must be such that the graduations would be so spaced as to be easily read; (4) since the error in weighing is inversely proportional to the size of the sample, the weight of the sample must be as great as possible while still conforming to the other requirements.

The Babcock centrifuges now on the market limit test bottles, so far as total length is concerned, to two types, known respectively as 6-inch and 9-inch bottles. In graduating a test bottle of either of these types, it is obvious that if results are to be read directly in terms of percentage of butterfat, the neck of the bottle must, for easy manipulation, hold a quantity of fat from an 18-gram sample somewhat in excess of the maximum percentage of fat that is likely to occur in butter. The average fat content of butter is about 82.5 per cent, while the maximum fat content is not likely to exceed 85 per cent. It can therefore be assumed that a bottle with a maximum reading of 90 per cent would be adequate for butter samples containing high percentages of fat and at the same time would allow for some error in filling and manipulating during the testing process.

In any Babcock bottle of the straight-necked type, one of the most important relations is that of the length of the graduated part of the neck to its diameter. With a given weight of sample, the long, slender neck will allow graduations to be well spaced, which means easy reading, while the short neck of large diameter for the same weight of sample means crowded graduations and difficult reading.

Types of bottles used

Four types of bottles, two 9-inch and two 6-inch, were developed which would meet the foregoing requirements. They are designated in the text as the 9-inch, 18-gram, 90-per-cent butter bottle; the 9-inch, 9-gram, 90-per-cent butter bottle; the 6-inch, 6-gram, 90-per-cent butter bottle; and the 6-inch, 5-gram, 90-per-cent butter bottle.

In a 9-inch, 18-gram, 90-per-cent bottle, the graduated part of the neck must have a capacity of exactly 90 per cent of the sample tested. With an 18-gram sample this would be 16.2 grams. The average specific gravity of butterfat under test conditions, however, is 0.9; therefore, 16.2 grams of butterfat will occupy a space of $16.2 \div 0.9 = 18$ cubic centimeters. The volume of the neck between the graduations 0 and 90 for this type of bottle must therefore be 18 cubic centimeters. In order to get this volume, in a practical bottle the length of the graduated part of the neck must be on the average 141 millimeters and the diameter must be 12.75 millimeters. It was soon discovered that this wide diameter contributed to rather large errors in reading, and the 18-gram bottle was therefore discarded.

Following the method of calculation used for the 18-gram bottle, the graduated part of the neck of a 9-inch, 9-gram, 90-per-cent bottle must have a volume of 9 cubic centimeters. This volume was secured in a type of bottle having approximately the following dimensions: height over all, 223.5 millimeters; length of graduated part of neck, 139 millimeters; diameter of graduated part of neck, 9.07 millimeters.

As already stated, some of the centrifuges in common use will not hold a bottle more than 6 inches long. It therefore seemed necessary to develop a bottle of such dimensions that it would fit the 6-inch centrifuge. This could be accomplished either by shortening the neck and increasing its diameter, and so keeping the size of the sample at 9 grams, or by reducing the size of the sample, which would allow both shortening the neck and reducing its diameter. In a 6-inch bottle the graduated part of the neck is limited to approximately 93.5 millimeters, which means that for a 9-gram sample the diameter must be 11.07 millimeters. Since the most satisfactory results are not obtained in cases in which the diameter of the neck exceeds 9.5 millimeters, it seemed best to cut the size of the sample to a point where a bottle with a neck approaching this diameter could be

used. This was attained in the 6-inch, 6-gram, 90-per-cent butter bottle of the following dimensions: height over all, 165.09 millimeters; length of graduated part of neck, 93.5 millimeters; diameter of graduated part of neck, 9.04 millimeters.

Several bottles of the 6-inch, 5-gram, 90-per-cent type were made for this investigation, but since the possibility of error was increased thru the use of a smaller sample, without materially improving the graduations, the results of the 5-gram bottle are not presented here.

Taking the sample

A discussion of any method of analysis of butter should include some facts concerning practical methods for sampling the product. Commercially this feature is a most vital one, and a disregard of these facts may lead to very erroneous results. Butter in the tub, in any finished package, or even in the churn, is not a homogeneous mass, and in this condition, unlike milk or cream, it cannot be readily mixed or stirred. The difficulty of securing representative samples from such packages has been shown by Guthrie and Ross (1913) and by Lee, Hepburn, and Barnhart (1909). It is noticeable that more uniform and representative samples can be obtained from the over-worked butter usually found in the manufacturing plants of Illinois than from medium or under-worked butter.

Sampling from the churn.— Since butter as found in the churn is not homogeneous even after the washing process is completed (Guthrie and Ross, 1913), any effort to secure a representative sample must necessarily result in a sample which approximates the composition of the total mass rather than one which actually represents it. Creamery control samples are usually taken from the churn by the following method: the surface of the butter for the full length of the churn is first removed with a ladle; then, by means of a spatula or a spoon, at least ten samples are transferred from points about equally distributed between the two ends of the churn, to make up the composite sample in a 5- to 8-ounce glass-stoppered bottle. It is obvious that the greater the number of small samples and the larger the composite, the more likely the composite is to represent accurately the butter in question.

Sampling from the tub.— Securing an accurate sample of butter from the tub is even more difficult than getting one from the churn. Many methods

have been suggested for obtaining representative composites, but any one of these methods may under certain conditions result in considerable variation. In sampling butter in this condition, it is usually desirable to take the sample in such a manner that the original neat appearance of the package will be maintained. For this purpose the ordinary butter-trier method is generally used. Usually two triers, spaced about equidistant from the center of the tub, are drawn, representing the full depth of the tub. These samples are then transferred to the glass container with as little loss of moisture as possible.

Preparing the sample for analysis

Assuming that the sample under observation has been collected in the glass-stoppered bottle just previous to analysis, it is placed in a warming pan where it is held until the butter assumes a semi-liquid condition. Warming should be accompanied by frequent shaking. In this condition the butter constituents may separate, and the problem is to get them back into a complete mixture approaching emulsion. This is accomplished by a gradual cooling of the sample, accompanied by almost constant and vigorous agitation. When the mixture has reached a condition approaching the consistency of very thick cream, it is in proper condition for sampling for analysis.

A second method of preparing the sample is by the use of a mechanical stirrer. This method is frequently employed in commercial plants, where speed is a considerable factor in the determination.

Making the test with the 9-inch, 9-gram, 90-per-cent bottle

When the butter has attained the consistency described above, a 9-gram sample is weighed into the butter bottle. This transfer to the test bottle should be made by pouring directly rather than by the use of a pipette. A scale as sensitive as that commonly used for moisture testing in butter should be used.

The sample having been weighed into the test bottle, 9 cubic centimeters of lukewarm water is added, followed by 17.6 cubic centimeters of commercial sulfuric acid. Extreme care must be exercised in adding the acid because of the violent reaction which frequently takes place between the acid and the salt in the butter, causing foaming and occasionally the

loss of the sample. To avoid this difficulty the acid should be added in small portions, and mixed thoroly after each addition, until finally the 17.6 cubic centimeters has been added. After the sample has been thoroly mixed with the acid, water is added in sufficient quantity to fill the bottle to the base of the neck. (It is obvious that less than 17.6 cubic centimeters of acid would dissolve all the solids in butter; one distinct advantage of adding a larger amount of acid, however, is that it is desirable to have considerable liquid of high specific gravity in the test bottle to insure a more complete separation of the fat.) The bottle is then placed in the tester and centrifuged for a period of five minutes at the same rate of speed that is used in testing milk and cream. Water is then added to bring the fat up within the graduated part of the neck, and the sample is centrifuged for four minutes.

Reading the test.— Samples are transferred from the tester to a reading bath and tempered at from 125° to 130° F. The best results are obtained by removing the meniscus with glymol (Hunziker and others, 1910). The results are read directly in terms of percentage of butterfat.

Making the test with the 6-inch, 6-gram, 90-per-cent bottle

The preceding directions for testing with the 9-inch, 9-gram, 90-per-cent bottle are followed in detail with the 6-inch, 6-gram, 90-per-cent bottle with two changes; first, 6 grams instead of 9 grams of butter are weighed with the test bottle; secondly, 12 cubic centimeters of water is added just previous to the introduction of the acid.

RESULTS OF THE EXPERIMENT

The reliability of this method of testing is shown by a comparison of the results obtained thru its use with the results obtained by chemical analyses on the same samples. The samples of butter under consideration were tested in the 9-inch, 9-gram bottle and the 6-inch, 6-gram bottle by the author, after which they were given to another operator who performed similar tests on the same samples. These samples are characterized in the data as original and check samples, respectively. All results were finally compared with the chemical analyses.[3] The results are presented in the form of direct comparison and also in the form of correlation tables.

[3] The chemical analyses were made by J. M. Barnhart and Dr. E. F. Kohman, dairy chemists, Agricultural College, University of Illinois. They were made according to the indirect official method as described in Bulletin 107 of the United States Bureau of Chemistry.

The results of the work of two operators on the same sample of butter, compared with the results obtained by a chemist on the same sample, are given in table 2:

TABLE 2. RESULTS OF THE MODIFIED BABCOCK METHOD COMPARED DIRECTLY WITH RESULTS OBTAINED BY CHEMICAL ANALYSIS

(Expressed in percentage of butterfat)

Test no.	6-gm. 6-in. (N. W. H.)	9-gm. 9-in. (N. W. H.)	9-gm. 9-in. (L. R. L.)	9-gm. 9-in. (L. R. L.)	6-gm. 6-in. (L. R. L.)	Chemical analysis
1	79.75	80.00	79.50	79.50	79.50	78.74
2	82.50	83.00	82.75	82.50	83.00	82.56
3	80.00	80.00	80.00	79.50	80.00	79.95
4	85.50	85.50	85.50	85.25	85.00	85.08
5	83.50	83.50	83.00	83.50	83.00	82.50
6	84.50	84.50	84.50	84.50	84.50	84.50
7	84.00	84.50	83.50	83.50	84.00	84.00
8	82.50	82.50	82.50	83.00	83.00	83.00
9	82.50	82.50	82.50	82.50	83.00	83.00
10	84.50	84.50	85.50	85.00	85.00	85.00
11	83.00	....	84.25	84.00	83.50	83.75
12	83.00	....	83.50	84.00	83.50	83.37
13	78.50	....	78.50	79.50	78.50	78.57
14	80.50	....	81.00	81.00	80.75	81.19
15	75.50	....	75.50	75.50	75.50	75.47
16	82.50	82.75	82.50	83.00	....	81.98
17	82.00	82.00	82.00	81.50	....	80.86
18	83.50	83.25	83.00	83.25	....	82.61
19	82.50	82.25	83.00	82.50	....	82.51
20	83.25	83.50	83.50	83.00	....	82.88
21	80.50	80.50	80.75	....	80.50	81.08
22	76.00	76.25	76.25	....	76.25	76.25
23	80.00	80.00	80.00	....	80.00	80.60
24	79.50	79.50	79.50	....	79.50	79.68
25	82.50	82.25	82.25	....	82.00	82.06
26	81.75	81.75	81.50	....	81.50	80.09
27	81.50	82.00	80.00	....	81.50	80.85
28	79.25	79.00	79.00	....	78.00	78.39
29	80.00	80.25	80.00	....	80.00	80.33
30	80.00	81.00	79.50	....	79.50	80.36
31	80.50	80.25	80.25	....	80.50	80.68
32	81.75	81.50	81.50	....	81.50	81.21
33	83.00	83.00	82.50	....	82.25	82.87
34	80.50	80.50	80.50	....	81.00	81.17
35	82.50	82.25	82.25	....	82.00	82.06
36	78.60	78.80	78.50	....	78.75	78.77
37	81.25	81.50	81.25	....	81.75	81.67
38	85.00	85.00	....	....	....	85.26
39	84.50	84.00	....	....	....	84.60

TABLE 2. RESULTS OF THE MODIFIED BABCOCK METHOD COMPARED DIRECTLY WITH RESULTS OBTAINED BY CHEMICAL ANALYSIS (*continued*)

(Expressed in percentage of butterfat)

Test no.	6-gm. 6-in. (N. W. H.)	9-gm. 9-in. (N. W. H.)	9-gm. 9-in. (L. R. L.)	9-gm. 9-in. (L. R. L.)	6-gm. 6-in. (L. R. L.)	Chemical analysis
40	79.50	79.60	....	....	....	80.00
41	82.00	82.00	....	....	....	82.18
42	76.25	76.50	....	....	....	76.29
43	80.50	80.50	....	....	....	80.24
44	....	83.25	83.50	....	....	83.22
45	84.50	84.50	84.50	....	84.50	84.64
46	84.00	84.50	83.50	....	84.00	84.16
47	82.50	82.50	82.50	....	83.00	82.40
48	82.50	82.50	82.50	....	83.00	82.40
49	84.50	84.50	85.50	....	85.00	84.66
50	85.00	85.25	85.00	....	84.50	84.87
51	83.00	83.00	82.50	....	83.00	82.83
52	79.75	79.00	79.75	....	80.00	79.73
53	85.50	85.00	85.50	....	85.25	86.66
54	82.50	83.00	82.50	....	83.00	82.34
55	84.25	83.50	83.00	....	83.00	83.60
56	85.00	85.25	85.00	....	84.50	84.79
57	82.50	82.50	82.00	....	82.00	81.97
58	83.00	83.50	84.00	....	84.00	83.32
59	82.00	82.00	82.50	....	83.00	82.39
60	80.00	79.75	77.75	....	....	77.68
61	....	83.50	....	....	....	83.95
62	85.50	85.50	85.75	....	....	86.00
63	82.50	85.50	....	....	....	82.93
64	82.00	....	82.50	....	....	82.80
65	....	....	82.50	....	....	81.93
66	....	....	83.00	....	....	82.12
67	....	....	83.00	....	82.50	81.69
68	....	....	82.50	....	82.50	82.09
69	....	....	83.00	....	83.00	82.00
70	....	....	82.00	....	81.50	81.63
71	....	....	82.00	....	81.50	81.73
72	....	....	82.25	....	81.50	81.69
73	82.00	....	82.50	....	81.75	81.83
74	81.75	81.25	82.50	....	82.50	81.49
75	....	81.00	82.00	....	81.50	81.55
76	81.00	81.50	81.50	....	81.50	81.06
77	80.50	80.00	....	....	80.50	80.36
78	80.50	81.00	81.50	....	81.00	80.36
79	81.00	80.50	81.00	....	80.50	80.30
80	81.50	81.50	81.25	....	81.25	80.99
81	81.50	82.00	....	....	....	81.76
82	82.00	82.25	82.00	....	81.50	80.70
83	81.50	81.25	81.50	....	81.00	80.61

TABLE 2. RESULTS OF THE MODIFIED BABCOCK METHOD COMPARED DIRECTLY WITH RESULTS OBTAINED BY CHEMICAL ANALYSIS (*concluded*)

(Expressed in percentage of butterfat)

Test no.	6-gm. 6-in. (N. W. H.)	9-gm. 9-in. (N. W. H.)	9-gm. 9-in. (L. R. L.)	9-gm. 9-in. (L. R. L.)	6-gm. 6-in. (L. R. L.)	Chemical analysis
84	80.00	80.50	....	....	....	78.82
85	84.50	84.00	....	....	....	83.98
86	78.50	78.50	....	....	....	77.82
87	82.00	82.50	....	....	....	81.46
88	80.50	80.25	....	....	....	80.42
89	81.00	81.00	....	....	....	81.84
90	82.00	82.00	....	....	....	82.30
91	82.00	81.75	....	....	....	82.91
92	82.00	82.50	....	....	....	82.22
93	79.00	79.00	....	....	....	79.07
94	85.00	84.50	....	....	....	85.09
95	79.00	79.50	....	....	....	79.17
96	81.50	81.50	....	....	....	80.80
97	81.50	82.00	....	....	....	81.25
98	83.50	83.25	....	....	....	83.69
99	83.25	83.25	....	....	....	83.26
100	83.00	83.50	....	....	....	82.13
101	80.50	81.50	....	....	....	81.79
102	81.50	82.00	....	....	....	80.40
103	80.50	80.75	....	....	....	79.47
104	84.50	84.00	....	....	....	83.64
105	83.50	83.50	....	....	....	84.08
106	81.25	82.00	....	....	....	80.65
107	81.00	81.00	....	....	....	81.39
108	82.00	82.75	....	....	....	81.45
109	81.50	82.00	....	....	....	81.65
110	79.50	....	....	....	....	79.45
111	80.75	81.50	....	....	....	79.68
112	83.00	83.50	....	....	....	83.50
113	83.00	83.50	....	....	....	83.52
114	80.00	81.00	....	....	....	81.03
115	83.50	82.75	....	....	....	82.47
116	82.00	82.50	....	....	....	82.57
117	79.50	79.50	....	....	....	80.69
118	82.00	82.50	....	....	....	82.42
119	....	82.00	82.00	81.75	82.00	82.02
120	....	78.00	78.00	78.00	78.00	78.33
121	....	85.25	85.25	85.00	85.25	84.99
122	....	80.00	80.00	80.00	....	80.48
123	....	80.00 79.50	79.75 80.00	80.00	79.50	80.21
124	....	79.50 79.75	79.50	79.50 79.75	79.50	80.25

The performance of the above described tests, as well as chemical analyses on the same 124[4] samples of butter, has resulted in considerable data from which an estimate of the relative accuracy of these tests may be obtained. In order to get some mathematical expression with which to show how nearly the results from the two methods are in agreement, certain statistical methods involving correlation coefficients are applied. The mathematical expressions employed in this work have already been used to a considerable extent in agricultural literature, for the purpose of presenting the results of rather complicated statistical investigation (Davenport 1907, Davenport and Rietz 1907, Rietz and Smith 1910).

The data for each type of bottle, including both original and check tests, are tabulated also in the form of separate correlation tables. These correlation tables may be regarded as double-entry tables in which the data are classified with respect to both chemical analyses and modified Babcock tests. As an illustration of the meaning of the figures in the correlation tables, the number *2* in the fourth row, third column, of table 3 means that there are two cases out of 124 in which the result of the chemical analysis falls within the interval 78–78.9 and the corresponding result for the modified Babcock test falls within the interval 79–79.9.

The correlation tables representing, respectively, the various methods under discussion, together with the checks, exhibit the original data from which are derived the mathematical expressions denoting the merits of the modified Babcock method. These expressions are the mean, designated by m; the coefficient of correlation, designated by r; the standard deviation, designated by t; and the coefficient of variability, designated by C. Since the coefficient of correlation in general may be understood as the numerical measure of the interrelations between different characters, it may be used in this instance as an expression to indicate how closely the results obtained by the modified Babcock method follow the results obtained by chemical analysis.

The first comparison considered is that of the results of the modified Babcock test using 6-inch, 6-gram bottles, with the results obtained from chemical analysis (table 3). When these tests are applied to the same

[4] Comparisons on more than double this number of samples were made at various times, but in presenting the data by the statistical method only those in which the data are complete with reference to the 9-inch, 9-gram, and the 6-inch, 6-gram, checks and chemical analyses, could be used.

TABLE 3. CORRELATION BETWEEN PERCENTAGE OF BUTTERFAT OBTAINED BY CHEMICAL ANALYSIS, SUBJECT, AND PERCENTAGE OF BUTTERFAT BY THE MODIFIED BABCOCK TEST, RELATIVE. SIX-INCH, SIX-GRAM BOTTLES

	76–76.9	77–77.9	78–78.9	79–79.9	80–80.9	81–81.9	82–82.9	83–83.9	84–84.9	85–85.9	86–86.9	
76–76.9	2											2
77–77.9		1										1
78–78.9		1	4									5
79–79.9			2	6	3							11
80–80.9		1	1	3	11	6						22
81–81.9					6	11	1					18
82–82.9					3	3	17	4				27
83–83.9							8	10	2			20
84–84.9								3	5	1		9
85–85.9							1		2	4	2	9
	2	3	7	9	23	20	27	17	9	5	2	124

124 samples of butter, the means and variabilities for and the correlations between the chemical analysis and the 6-inch, 6-gram analysis are as follows:

Babcock test	Chemical analysis
m = 81.91 ± .12	m = 81.72 ± .12
t = 1.97 ± .08	t = 2.02 ± .09
C = 2.41 ± .11	C = 2.47 ± .11

r = .935 ± .008

The mean percentage of butterfat in all the samples by chemical analysis is found to be 81.72 ± .12, while by the modified Babcock method (6-inch, 6-gram bottles) it is 81.91 ± .12. This is a difference of 0.19 per cent in the means. Since the probable error of each of the means, 0.12, is nearly as great as the difference between the means, no significant difference is shown to exist between the means of the results from each method. The standard deviations, 2.02 ± .09 for the chemical analysis and 1.97 ± .08 for the 6-inch, 6-gram analysis, show no significant difference, as is also the case with the coefficients of variability, 2.47 ± .11 for the chemical analysis and 2.41 ± .11 for the 6-inch, 6-gram bottle. The fact that these two measures of variability exhibit no significant differences is still further evidence that the two methods of analysis yield results which are almost identical and are for all practical purposes interchangeable.

To determine the correlation between individual results from chemical analyses and those obtained from the modified Babcock method, the correlation coefficient, r, is employed. This coefficient is a number whose value is not greater than 1 nor less than -1. A perfect positive correlation is given by $r = 1$, no correlation by $r = 0$, and a perfect negative correlation by $r = -1$. The correlation coefficient for the data in table 3, representing 124 samples, is $0.935 \pm .008$. Since this is a very high degree of correlation, the evidence is positive that the two methods of analysis yield results almost identical.

An examination of table 3 itself throws further light on the agreement of these results. It will be observed that the numbers arrange themselves very close to a diagonal running from the upper left corner to the lower right corner. If the results of the modified Babcock method and those of chemical analysis had been in exact agreement, the numbers would fall exactly on such a diagonal. The fact that they fall so close to this diagonal indicates that a high degree of correlation exists. Taking as a basis an assigned interval of 1 per cent in the tabulation of the results from the chemical analysis, it is seen that the variation in the modified Babcock test is confined to a very narrow limit. Out of a total of 124 comparisons, the two sets of results differ by 0.5 per cent or less in 78 cases, by 1 per cent or less in 113 cases, and by less than 2 per cent in 123 cases.

TABLE 4. Correlation between Percentage of Butterfat Obtained by Chemical Analysis, Subject, and Percentage of Butterfat by the Modified Babcock Test, Relative. Nine-Inch, Nine-Gram Bottles

	76–76.9	77–77.9	78–78.9	79–79.9	80–80.9	81–81.9	82–82.9	83–83.9	84–84.9	85–85.9	86–86.9	
76–76.9	2											2
77–77.9		1										1
78–78.9		1	2									3
79–79.9		1	2	4	3							10
80–80.9			3	1	10	3						17
81–81.9				1	5	11	1					18
82–82.9					6	8	12	2				28
83–83.9							11	8	1			20
84–84.9								4	5	2		11
85–85.9									2	3	2	7
	2	3	7	6	24	22	24	14	8	5	2	117

The correlation between the results from the modified Babcock test using 9-inch, 9-gram bottles, and the results from chemical analysis, is shown in table 4. The means and variabilities for and the correlation between these results are as follows:

Babcock test		Chemical analysis
$m = 82.04 \pm .12$		$m = 81.68 \pm .13$
$t = 1.91 \pm .08$		$t = 2.03 \pm .09$
$C = 2.33 \pm .10$		$C = 2.49 \pm .11$
	$r = .918 \pm .010$	

A difference of $0.36 \pm .17$ is found to exist between the two means. This difference, while small, indicates a possible tendency for the 9-inch, 9-gram bottles to yield results slightly higher than those from the chemical analysis. The difference is not great enough, however, in the light of the probable error, to be regarded as significant. The two measures of variability also point to a very close agreement between the results of the two methods of analysis.

The data in table 4, like those in table 3, tend toward an arrangement in a diagonal of rather narrow limits. Mathematically the correlation is $0.918 \pm .010$. In 73 cases the results obtained by the modified Babcock method with the 9-inch, 9-gram bottles differ from those of chemical analysis by less than 0.5 per cent; in 99 cases the difference is less than 1 per cent; in 111 cases it is less than 1.5 per cent; and in 117 cases it is less than 2 per cent. On the basis of the data obtained, the two methods may be considered as yielding results which are for practical purposes identical.

Comparing the correlation coefficient for the results obtained with the 6-inch, 6-gram bottles and chemical analysis ($0.935 \pm .008$) with the correlation coefficient for the results with the 9-inch, 9-gram bottles and chemical analysis ($0.918 \pm .010$), it may be noted that there is a difference of $0.017 \pm .013$ between the two correlations.

It will be remembered that check tests were made by having the same samples tested by another operator. The relation existing between such checks and the originals when 6-inch, 6-gram bottles were used is shown

TABLE 5. Correlation between Percentages of Butterfat Obtained Respectively by Two Operators Applying the Modified Babcock Test with Six-Inch, Six-Gram Bottles to the Same Samples of Butter. Check Tests, Subject; Original Tests, Relative

	76–76.9	77–77.9	78–78.9	79–79.9	80–80.9	81–81.9	82–82.9	83–83.9	84–84.9	85–85.9	
76–76.9	1										1
77–77.9											0
78–78.9			4								4
79–79.9			1	3							4
80–80.9				1	10	2					13
81–81.9					1	8	2				11
82–82.9						2	2	5			9
83–83.9							1	5			6
84–84.9									4	2	6
85–85.9										3	3
	1	0	5	4	11	12	5	10	4	5	57

in table 5. The means and variabilities for and the correlations between these results are as follows:

Original tests	Check tests
m = 81.68 ± .18	m = 81.77 ± .19
t = 1.97 ± .12	t = 2.10 ± .13
C = 2.41 ± .15	C = 2.57 ± .16

r = .973 ± .005

In this case the two means show a difference of 0.09, which is approximately one-half the probable error of either mean. Consequently the means may be said to show no significant difference and for practical purposes may be considered identical. The standard deviations and the coefficients of variability, which are the measures of variability, also show no significant differences.

There is a somewhat higher degree of correlation between the results of the 6-inch, 6-gram original and check tests (table 5) than between the results of the 6-inch, 6-gram test and the chemical analysis (table 3). The figures for the former tend to fall into relatively small assigned classes, and form an almost perfect diagonal from the upper left to the lower right of the table. For the comparison of 6-inch, 6-gram originals with 6-inch, 6-gram checks, the correlation coefficient is 0.973 ± .005; while

for the comparison of 6-inch, 6-gram originals with the chemical analysis, the correlation coefficient is 0.935 ± .008. This is a difference of 0.038 ± .009. These results would seem to indicate that a closer agreement exists between the results of duplicates on the 6-inch, 6-gram bottles than between the results of the modified Babcock test with 6-inch, 6-gram bottles and the chemical analysis.

TABLE 6. CORRELATION BETWEEN PERCENTAGES OF BUTTERFAT OBTAINED RESPECTIVELY BY TWO OPERATORS APPLYING THE MODIFIED BABCOCK TEST WITH NINE-INCH, NINE-GRAM BOTTLES TO THE SAME SAMPLES OF BUTTER. CHECK TESTS, SUBJECT; ORIGINAL TESTS, RELATIVE

	76–76.9	77–77.9	78–78.9	79–79.9	80–80.9	81–81.9	82–82.9	83–83.9	84–84.9	85–85.9	
76–76.9	2										2
77–77.9		1									1
78–78.9			2								2
79–79.9			1	3							4
80–80.9				3	8	1					12
81–81.9				1		8	2				11
82–82.9					1		14	2			17
83–83.9							3	9	1		13
84–84.9								3	4	1	8
85–85.9										7	7
	2	1	3	7	9	9	19	14	5	8	77

The comparative results on check and original tests when 9-inch, 9-gram bottles are used are shown in table 6. The means and variabilities for and the correlations between these results are as follows:

Original tests	Check tests
m = 82.16 ± .16	m = 82.07 ± .16
t = 2.06 ± .11	t = 2.13 ± .12
C = 2.51 ± .14	C = 2.50 ± .14

r = .964 ± .005

The means for the original and the check tests with the 9-inch, 9-gram bottles also show no significant difference. The same is true of the standard deviations and the coefficients of variability.

The correlation coefficient for the data presented in table 6 is 0.964 ± .005. This coefficient, like that representing the comparisons with checks in the case of the 6-inch, 6-gram samples (table 5), indicates a

very high degree of correlation. Evidence of close checking is further substantiated by the fact that there is no significant difference in the means, the standard deviations, or the coefficients of variability. As previously shown, the coefficient of correlation between results of the modified Babcock test with 9-inch, 9-gram bottles and chemical analysis is 0.918 ± .010 (table 4), and that for the 9-inch, 9-gram originals and checks is 0.964 ± .005, a difference of 0.046 ± .011. This difference indicates that there is a higher degree of correlation between the original and the check tests than between the results of the modified Babcock test with the 9-inch, 9-gram original and the chemical analysis. It will be remembered that an analogous result was obtained in the case of the 6-inch, 6-gram bottles.

With the 9-inch, 9-gram bottles, about the same degree of accuracy is shown in the duplicates as that existing in the case of the 6-inch, 6-gram bottles. The results shown in table 6 emphasize the possibility of securing good checks when duplicate determinations are made by different operators. This, it should be noted, is a more difficult kind of check than that of duplicate determinations by the same operator.

The foregoing data show the close relationship that exists between the results obtained from comparisons of the modified Babcock test for 6-inch, 6-gram bottles with chemical analysis, and of the modified Babcock

TABLE 7. Correlation between Percentages of Butterfat Obtained by Applying the Modified Babcock Test with Six-Inch, Six-Gram Bottles (Subject) and with Nine-Inch, Nine-Gram Bottles (Relative) to the Same Samples of Butter

	76–76.9	77–77.9	78–78.9	79–79.9	80–80.9	81–81.9	82–82.9	83–83.9	84–84.9	85–85.9	
76–76.9	2										2
77–77.9		1									1
78–78.9			3	1							4
79–79.9				7	3						10
80–80.9				2	13	6					21
81–81.9					1	11	7				19
82–82.9						1	21	3			25
83–83.9								16	2		18
84–84.9								1	8		9
85–85.9									1	7	8
	2	1	3	10	17	18	28	20	11	7	117

test for 9-inch, 9-gram bottles with chemical analysis. Interesting comparisons may be made also between the results obtained with the 6-inch, 6-gram bottle and those obtained with the 9-inch, 9-gram bottle. Such comparisons are presented in table 7. The means and variabilities for and the correlation between these results are as follows:

Six-inch, six-gram bottles		Nine-inch, nine-gram bottles
$m = 81.90 \pm .12$		$m = 82.04 \pm .12$
$t = 1.95 \pm .09$		$t = 1.91 \pm .08$
$C = 2.38 \pm .004$		$C = 2.33 \pm .10$
	$r = .966 \pm .004$	

These data show that there is about the same degree of accuracy when samples are tested with 9-inch, 9-gram bottles as exists when the same samples are tested with 6-inch, 6-gram bottles. From the operator's point of view, however, the 9-inch, 9-gram bottle is preferable since it is more easily read and manipulated.

APPLICATION OF THE RESULTS

Checking plant operations

Urged by the increased pressure of a more aggressive competition, plant managers and manufacturers are realizing anew the importance of accurate plant checks for the purpose of controlling inefficiency and losses in manufacture. Within the plant there are three possible points of check on butterfat. The first of these occurs when the cream comes into the plant, at which time a determination is made of the total butterfat received. The second occurs when the cream is assembled in the ripeners. It is obvious that at this point the total butterfat in the ripeners should equal the sum of all butterfat paid for by the plant for any given period, minus any reasonable losses occasioned by the handling and pasteurizing processes. The third and last opportunity for a check, and one that is usually overlooked, is at the point when the butter is collected in the churn just previous to being packed. A fat determination at this point will yield a result representing the total butterfat recovered in the butter; that is, the total number of pounds of butter in the churn multiplied by its fat percentage will represent the total fat recovered

in the butter, and this figure should check with the ripener determination for fat for a given amount of cream, and in turn with the fat purchased for that churning.

Such checks were made at the University of Illinois creamery for a period of one year, and some of the typical results are here presented to illustrate the practicability of such a system of plant-check records. The figures

TABLE 8. Results of Creamery Plant Checks

Check no.	Fat bought (pounds)	Fat in ripener (pounds)	Butter (pounds)	Fat recovered in butter	
				Per cent	Pounds
1	333.1	337.4	421	80.00	336.6
2	316.7	314.6	377	82.50	311.0
3	445.1	440.2	545	80.00	436.0
4	327.0	324.0	408	81.00	325.6
5	208.6	203.4	255	82.50	210.3
6	307.0	309.6	375	82.50	309.0
7	327.0	321.0	395	81.75	323.9
8	247.7	247.3	310	80.00	248.0

(table 8) are suggestive of the possibility that exists for making more complete plant check records. This system is followed to some extent at the present time in some of the larger manufacturing plants of the United States.

Legal considerations

The legal regulations under which butter manufacturers now operate are given in an Act of Congress dated August 2, 1886, Section 1, as follows:

Butter defined: that for the purpose of this Act, the word butter shall be understood to be the food usually known as butter, and which is made exclusively from milk or cream or both, with or without common salt, with or without the addition of coloring matter.

Butter is further defined by an Act of Congress, approved May 9, 1902, as

the clean, non-rancid product made by gathering in any manner the fat of fresh or ripened milk or cream into a mass, which also contains a small portion ot the other milk constituents, with or without salt, and contains not less than eighty-two and five-tenths (82.5) per cent of milk fat.

The following paragraph is taken from page 87 of Regulations No. 9, revised July, 1907, United States Internal Revenue:

The definition of adulterated butter as contained in the Act of May 9, 1902, embraces butter in the manufacture of which any process or material is used whereby the product is made to contain abnormal quantities of water, milk, or cream; but the normal content of moisture permissible is not fixed by the act. This being the case it becomes necessary to adopt a standard for moisture in butter, which shall in effect represent the normal quantity. It is, therefore, held that butter having 16 per cent or more of moisture contains an abnormal quantity and is classed as adulterated butter.

The paragraphs just quoted constitute the essentials of the regulations under which butter manufacturers now operate. The fat standard of 82.5 per cent, however, has never been enforced. This has left in operation the ruling of the Internal Revenue Department demanding in substance that butter containing more than 16 per cent of moisture be considered adulterated. This has been the manufacturer's working basis for more than fifteen years, and it is just now coming to be realized that this enforced ruling in many ways does not fulfill all the requirements for a standard. Serious consideration has been given both by the law makers and by the manufacturers to the question of changing this ruling, and the most representative expression of these bodies at this time seems to be that placing a maximum on one of the nonessential ingredients in butter does not adequately control the product, either by way of protecting the consumer or by way of protecting the manufacturer from unjust competition. The sentiment at the present time, therefore, seems to favor a minimum legal fat content of 80 per cent in butter. If this ruling is put into effect, a new demand is at once created for a method of quickly determining fat in butter.

SUMMARY

The securing of a representative sample is one of the most important, as well as one of the most difficult, factors in making butter analyses.

Consistent duplicates and accurate results can be obtained only when a system of careful preparation of the sample is followed.

In a modified Babcock method of butter analyses, the test bottles should be so constructed that readings for percentage of fat are made directly.

In this investigation the 9-inch, 9-gram, 90-per-cent bottles and the 6-inch, 6-gram, 90-per-cent bottles were found to be the most satisfactory

types. From the standpoint of manipulation, the 9-inch, 9-gram bottle, permitting of a larger sample and better-spaced graduation, is the more desirable of these two.

The method of testing butter for fat, outlined in the text, yields results on the 124 samples which correspond very closely with those obtained by chemical analysis.

There was practically no difference between the results obtained with the 9-inch, 9-gram, 90-per-cent bottle and those obtained with the 6-inch, 6-gram, 90-per-cent bottle.

Check tests made by independent operators yield results which correspond more closely with each other than do the results on the respective bottles with chemical analyses.

ACKNOWLEDGMENTS

The author wishes to acknowledge the assistance rendered by H. A. Ruehe and L. R. Lang, who at various times have taken part in making check tests recorded in this thesis. Valuable suggestions were given also by F. A. Pearson in the presentation of tabular material, and by Louis F. Nafis, manufacturer of Babcock glassware, who furnished the glassware in connection with the development of the butter-test bottles.

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CORNELL UNIVERSITY

AGRICULTURAL EXPERIMENT STATION

THE CRANE-FLIES OF NEW YORK

PART II. BIOLOGY AND PHYLOGENY

CHARLES PAUL ALEXANDER

ITHACA, NEW YORK
PUBLISHED BY THE UNIVERSITY

THEODOR BELING
(1816–1898)

KARL WILHELM THEODOR BELING

No sketch of the life of Theodor Beling, the great German student of the immature stages of the Tipuloidea, has ever appeared in English. It was with considerable difficulty that the writer was able to get into communication with relatives and friends of Beling and obtain the data presented herewith.*

Theodor Beling was born at Steterburg, in the Duchy of Brunswick, Germany, on March 26, 1816. He was a son of the district forester. From 1828 to 1834 he attended school at Wolfenbüttel. At Easter, 1834, he began his chosen career as a forester, having served his prescribed apprenticeship of two years with his father at Danndorf. He attended the Royal Saxon Academy at Tharand from 1836 to 1837, and in the following year visited the University of Göttingen to round out his technical training in various branches relating to forestry. Beling's career as a forester extends from Easter, 1834, to October 1, 1888, when he was officially retired with a pension. In April, 1861, he was made Master of the Forest, a position which he held until his retirement.

After his retirement from active public service, Beling long continued his vigorous researches afield and at home. When far advanced in years, he went alone on long trips to seek new stations for plants and to observe animal life in wood and field. He died on December 17, 1898, at Seesen, where much of his finest work was accomplished.

During his lifetime Beling published one hundred and seven articles. The series of three papers which rank him as a pioneer in the field of crane-fly biology were published in the years 1873, 1879, and 1886, respectively. In these papers the histories of sixty-nine species of crane-flies are discussed in detail, and brief notes on five additional species are included. The other published articles of Beling cover a remarkable range of subjects relating directly or indirectly to the science of forestry. His most important researches on the life histories of insects, in addition to those on the Tipuloidea, are on the coleopterous families Parnidae and Elateridae. His published articles are dated between 1850 and 1888, but practically all of his entomological studies were published in the seventies and eighties.

Beling's excellent collection of dried plants, mounted birds, and sections of various woods, and his cabinet of insects — the last-named including the types of several species described by himself and by others — are preserved in the collection of the Natural History Museum at Brunswick. It is understood that the insects in this collection, including the alcoholic larvae and pupae of the Tipuloidea, are still in excellent condition.

* Sincere thanks are here extended to the following persons, who have added materially to the value of this biographical notice:

Landesforstmeister K. Block, son-in-law of Beling, who published in April, 1899 (in *Allgemeinen Forst- und Jagd-Zeitung*), a complete obituary notice relating to his father-in-law, and to whom the writer is indebted for several additional unpublished notes and for the loan of the excellent portrait of Beling reproduced herewith.

J. Meerwartz, Director of the Natural History Museum at Brunswick, who has furnished data concerning the present condition of the collection of the immature stages of the Tipuloidea described by Beling, now preserved in the above-mentioned institution.

William Prindle Alexander and Elsa Müller Alexander, who have rendered valuable service in translating the account of Beling's life.

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THE CRANE-FLIES OF NEW YORK

PART II. BIOLOGY AND PHYLOGENY

THE CRANE-FLIES OF NEW YORK

PART II. BIOLOGY AND PHYLOGENY[1]

CHARLES PAUL ALEXANDER

A preliminary classification of the immature stages of the Tipulidae and related families, suggested to the writer by Dr. J. G. Needham in 1911, is presented in this memoir. But few of the sixty-odd families of Diptera, and comparatively few species of the Tipulidae, have as yet been studied from this viewpoint, and therefore the arrangement herein adopted must be considered as tentative. The majority of the specimens used in the study were reared in New York State, the crane-fly fauna of which is typical of a great area thruout northeastern North America. In 1913, thru the kindness of Dr. Charles D. Woods and Dr. Edith M. Patch, the writer was enabled to continue his investigations in Maine.

It is the writer's purpose to outline the morphological characters available for the classification of the larvae and the pupae, and to give preliminary keys for the separation of the various groups; such keys will, of necessity, require constant revision or complete remodeling with the accession of new life-history material, but it is at least hoped that they may furnish a basis for future investigation. The most important work on the European fauna, that of Theodor Beling (1873 to 1887),[2] is rendered incomplete by the total lack of illustration, the insufficiency of description of the details of the larval head, and the artificial nature of the keys. That this difficulty in using Beling's figureless descriptions is not confined to the writer is shown by the following criticism by one of his fellow-countrymen (Czizek, 1911:7):

> "Leider fehlen uns bis jetzt fast vollständig gute Abbildungen der Larven und Puppen, ein fühlbarer Mangel auch in Beling's Abhandlungen, da die genaueste Beschreibung das Bild nie ganz zu ersetzen vermag."

It is intended to include in this paper the following material:

1. Descriptions of all new life-history material available, with notes on the biology and occurrence of the species.

[1] Part I of *The Crane-Flies of New York*, dealing with distribution and taxonomy of the adult flies, was published in 1919 as Memoir 25 of the Cornell University Agricultural Experiment Station.

[2] Dates in parenthesis refer to *Bibliography and References Cited*, page 1019.

2. Brief summaries of published life histories of genera and important species not available for study as specimens and included here to complete the data.

3. Summaries and tabulations of life-history records, larval habitats, economic importance, and related subjects.

4. Keys to the families, tribes, and lesser groups.

The adult flies are not here considered in any detail, since they have been discussed by the writer in an earlier paper (Alexander, 1919 d).

The life histories remaining to be discovered in the Nearctic fauna are still numerous in species, tho few in genera. There are but four or five genera whose life histories when made known may upset the present ideas on arrangement. Until more is known of these missing groups, they must be classified according to the adult structure.

It will be noted that a number of important changes in nomenclature have been adopted in this paper. The system hitherto in vogue, based entirely on the structure of the imagines, was conceived by Osten Sacken and represented the culmination of research on the structure and affinities of the adult flies. A casual survey of the immature stages is sufficient to show the impossibility of many of the groups hitherto generally accepted. The principal modifications adopted in this paper are as follows:

1. The erection of the family Tanyderidae to receive the genera Tanyderus and Protoplasa. These had hitherto been placed with the Ptychopteridae, a group to which they are not closely allied.

2. The removal of the genus Trichocera from the Tipulidae to the Rhyphidae, and the inclusion of the latter family as one of the four existing families of crane-flies.

3. In the Tipulidae, the elimination of four tribes — Antochini, Limnophilini, Dolichopezini, and Ctenophorini — as being based on a conglomeration of forms referable to other tribes or else separated on an insufficient basis. The former tribe Antochini included members which the writer now refers to the Limnobiini (Antocha, Rhamphidia, Dicranoptycha, and other genera) and to the Eriopterini (Teucholabis, Elephantomyia); the Limnophilini are too close to the Hexatomini; and the tipuline forms constitute a very compact group which cannot well be subdivided into tribes.

4. The erection of nineteen subtribes, or divisions, to include lesser groups of genera within the tribes. In the following pages these are

treated in what seems to be their phylogenetic sequence from the generalized to the specialized.

The arrangement of families, subfamilies, and lesser groups may be summarized as follows:

Families	Subfamilies	Tribes	Subtribes	Representative genera
Eoptychopteridae (fossil)				Eoptychoptera
Architipulidae (fossil)				Architipula
Tanyderidae				Tanyderus
				Protoplasa
Ptychopteridae	Ptychopterinae			Ptychoptera
	Bittacomorphinae			Bittacomorpha
				Bittacomorphella
Rhyphidae	Rhyphinae			Rhyphus
	Mycetobiinae			Mycetobia
	Trichocerinae			Trichocera
Tipulidae	Limnobiinae	Limnobiini	Antocharia	Antocha
			Ellipteraria	Elliptera
			Limnobaria	Limnobia
				Dicranomyia
			Dicranoptycharia	Dicranoptycha
			Rhamphidaria	Rhamphidia
		Hexatomini	Ularia	Ula
			Epiphragmaria	Epiphragma
			Pseudolimnophilaria	Pseudolimnophila
			Dactylolabaria	Dactylolabis
			Limnophilaria	Limnophila
				Ulomorpha
			Hexatomaria	Eriocera
				Hexatoma
			Polymeraria	Polymera
		Pediciini	Adelphomyaria	Adelphomyia
			Pedicaria	Pedicia
				Dicranota
		Eriopterini	Eriopteraria	Erioptera
				Ormosia
			Elephantomyaria	Elephantomyia
		Styringomyiini		Styringomyia
	Cylindrotominae			Cylindrotoma
				Phalacrocera
	Tipulinae	Tipulini	Dolichopezaria	Dolichopeza
				Brachypremna
			Ctenophoraria	Ctenophora
				Tanyptera
			Tipularia	Tipula
				Nephrotoma

A permanent series of the immature stages of the species studied has been carefully preserved in the writer's collection, while additional material has been placed in the principal collections of the United States. A series of two hundred and seventy microscope slides showing details of structure of the larvae and the pupae has been prepared, representing some seventy species arranged in forty genera. The typical larvae and pupae (*nepionotypes* and *neanotypes*) have been designated and preserved in alcohol for future reference.

For the most part, the life histories discussed in this paper have not been described hitherto. Besides the reared material, the writer has in his collection a very large number of unknown larvae and pupae, many of them representing interesting and undescribed types. In this paper but three or four of these are considered, and these only because they introduce new features of organization (Eriopterine No. 1, Tipulini No. 1 and No. 2).

A vast amount of work remains to be done on the immature stages of crane-flies. Exact, detailed life histories of individual genera and species are especially needed and the reward for effort will undoubtedly be great. Nothing is known of the tropical and the antipodal faunas, and their life histories will probably be unraveled but slowly, due to the inaccessibility of most of the regions.

The majority of specimens studied in the preparation of this paper were reared by the writer during the past nine years. Many specimens were received from various sources, however, including many of the most desirable life histories, and these are herewith gratefully acknowledged:

Dr. James G. Needham, Ithaca, New York. The extensive collections received from Dr. Needham include the material described in the various Adirondack reports, as well as numerous previously unrecorded specimens. In addition, the writer has accompanied Dr. Needham on many of his field trips in quest of the immature stages of aquatic insects, and has received much encouragement and inspiration from this association.

Charles W. Johnson, Boston, Massachusetts. Immature stages of Aeshnasoma, Elephantomyia, Teucholabis, and other species.

The late Frederick Knab, Washington, D. C. Immature stages of *Rhipidia bryanti*, Elephantomyia, *Epiphragma solatrix*, and other species.

J. A. Hyslop, Hagerstown, Maryland. Longurio (larvae), Oropeza, Gnophomyia.

J. R. Malloch, Urbana, Illinois. *Rhipidia bryanti*.

C. T. Greene, Washington, D. C. Protoplasa (supposition).

H. L. Viereck, Washington, D. C. Protoplasa (supposition).

W. L. McAtee, Washington, D. C. Protoplasa (supposition); numerous larvae from the Pribilof Islands.

William Lundbeck, Copenhagen, Denmark. Helobia and other species.

Dr. C. Wesenberg-Lund, Hilleröd, Denmark. Phalacrocera, *Ptychoptera paludosa*, *Tipula maxima*, and other species.

William G. Dietz, Hazleton, Pennsylvania. Notes on larvae of *Dicranomyia macateei* Alex.
Oskar A. Johannsen, Ithaca, New York. *Limnobia fallax*, and other species.
Carl Ilg, Philadelphia, Pennsylvania. Notes on *Rhipidia fidelis*.
O. H. Swezey, Honolulu, Hawaii. Notes on Libnotes and Styringomyia.
H. K. Munro, Pretoria, Transvaal. Notes on Trentepohlia and Styringomyia.
Charles Bruch, La Plata, Argentina. Notes on Trimicra, Helobia, and Epiphragma.
D. B. Young, Albany, New York. Notes on Gnophomyia.
J. T. Lloyd, Cincinnati, Ohio. Eriocera.
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A. E. Cameron, Ottawa, Canada. *Cylindrotoma splendens*.
R. C. Shannon, Ithaca, New York. Elephantomyia, Brachypremna, *Tipula fuliginosa*, and other species.
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Harold Morrison, Washington, D. C. Holorusia, and *Tipula usitata*.
C. Hamilton Kennedy, Columbus, Ohio. Prionocera and Rhamphidia.
J. Chester Bradley, Ithaca, New York. Longurio.
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Further acknowledgments of assistance in determining plant and animal associates of crane-flies are made thruout the text. In conclusion, the writer expresses his indebtedness to his wife, Mabel M. Alexander, for her untiring care and assistance in the typing and final preparation of this thesis.

GENERAL CONSIDERATIONS

REPRESENTATIVE CRANE-FLY LIFE HISTORIES

The life histories of but few species of crane-flies have been studied in detail. The very nature of the habitat (mud or earth) required by most species of the family renders it a most difficult operation to rear the species from the egg to the adult and note the various stages, their molts, their habits, and other features. The subfamily Cylindrotominae, the immature stages of which live on the leaves of various higher plants and curiously resemble the caterpillars of certain Lepidoptera, furnishes species whose habits are more readily studied than most others, and as a result the immature stages of this group are better known, perhaps, than those of any other section of the family. Two widely different species have been chosen, and their life histories as they are known at present are here outlined. The first is a species of Eriocera, a powerful, semi-aquatic carnivore; the second is a species of Cylindrotoma, a terrestrial herbivore. In the text which follows, notes on the life activities of various other species are given, but the gaps in the knowledge of this phase of the subject are very considerable and there still remain innumerable interesting facts to be ascertained.

Eriocera longicornis (Walk.)

The common crane-fly *Eriocera longicornis* is widely distributed over the northeastern United States and Canada. Altho the species is local in its distribution, the flies may be found in abundance wherever it does occur. The situations that favor the presence of these flies are large streams or rivers with sand or gravel bottoms and banks. The following notes were taken, partly in Fulton County, New York, along the Sacandaga River, and partly in Tompkins County, along Fall and Cascadilla Creeks. Some of these data have already been published by Alexander and Lloyd (1914:12–18) and by the writer (Alexander, 1915 c:149–152).

On May 27, 1914, the adult flies were exceedingly numerous near the village of Northampton, Fulton County. They were present in untold myriads, and at every step they arose in clouds from under foot or from the leaves of chokecherry on which they rested. They sat on the leaves with the head directed away from the observer, ready to take instant flight, and at the first approach of a possible enemy they darted up into

the air and far overhead. A few were in copulation on the leaves, but from observations made later it seems probable that mating begins in the air and the united pair seek a support later on. Toward twilight the flies may be found in great numbers in company with many kinds of caddice flies and may flies. The swarms vary in numbers from about fifty individuals to those including many thousands. Some of the larger of these swarms cover a vertical height of at least fifty feet, the lower individuals being about fifteen feet above the water. When danger approaches, the swarm either mounts into the air overhead or retreats before the breeze, never advancing nor moving sidewise.

Out over the land in the smaller swarms, copulation was observed several times. The males in the swarm dart swiftly at the females and seize them almost instantly. They then usually leave the swarm and go sailing away, the male above doing the flying, the smaller female hanging limply beneath. The antennae of the male at this time are directed straight ahead and are slightly divergent, the legs hang downward, the wings vibrate rapidly. The female hangs downward with the legs trailing limply beneath, the wings nearly horizontal and motionless. The dead weight of the female continually pulls the male toward the water, and often both fall into the river. As a rule, copulation ends before the male is exhausted. The male opens his forceps and the female drops straight downward for a foot or so, quite like a parachute released from a balloon. If the pair are near the surface at the time of separation, the released female drops into the water. The male darts upward again and back into the swarm. The female slowly flies away, usually upstream but sometimes downstream, presumably to lay her eggs. She does not stop for swarms that she may encounter, and may even make a wide detour in order to avoid them. In a very few cases the female is the active partner and succeeds in pulling the male where she wills altho she is much smaller. No matings were observed during the hours of sunlight, and it was only at twilight or just after sunset that mating took place. Often a second male will seize a female already in copula and the three will come tumbling down into the water together. One such pairing of three individuals came down, and when they were about a foot above a board in the water the male in copulation dropped the other two. These rested for a moment, and then the remaining male attempted to engage the female in copulation. She resisted but finally he managed to seize her

with his forceps. Then he attempted to fly away, but she seized hold of the board with all her feet and he was unable to disengage her. This seems to indicate that the normal place for copulation is in the air.

The motions of the insects in the swarm were very rapid, almost like those of bees, and the sound produced was at a very low pitch, much lower than that made by Culex. The movements are on a horizontal plane, each individual flying mostly in the path of a figure 8, sometimes slowly and at other times much more rapidly.

Many specimens were seen dipping down into the water, as tho engaged in laying eggs. All of the few specimens captured proved to be males, but why this sex should go thru these motions is not clear to the writer. This action has been observed several times in various species of crane-flies. It is very probable that the female lays her eggs in the water in this manner.

The eggs are pale white or brown, not heavily chitinized as are those of Hexatoma but with the chorion feebly sculptured. They vary in number from 892 to 1034, with an average of 952. They are small, about the same size as those of Hexatoma. The ovaries almost completely fill the abdominal cavity, and the eggs are arranged in the ovaries like bananas on a stalk, with numerous pale nurse-cells in between.

The larval life is passed in streams, usually under rocks. The winter is spent in the larval condition, but the larvae do not attain full size until the following spring. At this time they come to the land and live in the sand and gravel along the banks of the streams. By the alternate extension and contraction of the body and the inflation of the penultimate segment of the abdomen at the moment of extension, the larvae are capable of inflating this segment into an enormous globular structure which serves as an aid to progression thru the soil. The food of the larvae consists largely of animal matter, and often large species, such as chironomid larvae, are swallowed whole. The almost total lack of chitinization of the mental region allows for great distension of this part of the body. The powerful mandibles and the retrorsely roughened esophagus serve the function of both holding the prey and preventing its ejection when once swallowed. Considerable gravel and particles of vegetable tissue are also found in the proventricular region.

When ready to transform to the pupal condition, the larva becomes sluggish. After molting the last larval skin, the pupa is disclosed, pale

yellowish white and very callow. The pupa forms burrows in the loose gravel, these being vertical, or, more often, a little oblique. The diameter of the burrow is a little greater than that of the pupa. The length varies, the burrow for a young pupa being a mere chamber inclosing the individual and located from one-half to one inch below the surface. As the pupa becomes older, by a bobbing up-and-down motion it lengthens the burrow upward until finally it penetrates the surface layer and forms a small shot-like opening. Here the pupa rests, often bobbing up and down with a rhythmic motion, but ducking down into the burrow when danger threatens. The length of the burrow is rarely more, but usually less, than twice the length of the pupa. A few of the pupae seem to be inclosed in a very delicate silken tube and the salivary glands seem to be well adapted for the purpose of forming silk; but the great majority of the pupae are entirely naked. The indoor pupal period varies from one hundred and seventy to one hundred and seventy-three hours, or a little more than seven days. The outdoor pupal period, however, is undoubtedly longer, unless the weather is very warm.

The emergence of the adults usually takes place during the late hours of the morning, the greatest number emerging between ten o'clock and noon. When ready to emerge, the pupa pushes part of its body out of the earth, the posterior two-thirds or half remaining attached to the soil. If it projects farther than this, its transformation seems to be a very difficult operation. The pupa bends backward and forward constantly, flexing the body dorso-ventrally. This motion appears to exhaust it, since it frequently rests. The skin splits lengthwise up the mesonotum and the adult emerges. The male has difficulty in extricating its very long antennae from their sheaths. The tips of the fore femora are placed underneath the sharp spines of the flagellum, and by raising the legs the insect pulls the antennae slightly outward. These spines are regularly spaced, and, since both fore legs work in unison, the spines function as cogs and the whole antenna is gradually forced from the pupal sheath. The body is carried very straight and stiff during the operation, and the abdomen is very long and pale. The drawing out of the extreme tips of the antennae is usually accomplished by the insect flexing its whole body backward. When the antennae are freed, the insect walks a few steps from the cast skin, withdrawing its abdomen from the case. (The emergence of *E. spinosa* is shown in Plate XII, 1.) A drop of nearly colorless liquid is excreted

from the body at this time. The teneral adult then waits quietly until it gains more strength and color. This condition of the insect is the most dangerous period of its existence, since it is defenseless against all enemies.

The insects are associated in the gravel with ground beetles of the genera Omophron, Schizogenius, Dyschirius, Bembidion, Tachistodes; with click beetles of the genus Cryptohypnus; and with rove beetles, of which Paederus, Lathrobium, and Gastrolobium are the commonest forms. In addition, numbers of larvae of Tabanidae, Leptidae (Atherix), *Eriocera spinosa, E. fultonensis, E. cinerea,* and *Erioptera armata* were found. Natural enemies of the pupae and the teneral imagines are the medium-sized black lycosid spiders, which preyed in numbers on the weak, uncolored adults. Dozens of these spiders were noticed with individuals of the crane-flies in their grasp. When alarmed they would run rapidly away, but only in exceptional cases would they release their victims. A few spiders of other families, notably the Attidae, were found with Eriocerae. Dragon-flies appear to be the most serious enemies of the active adults. *Helocordulia uhleri* (Selys) has been observed capturing the crane-flies by darting back and forth thru the swarms of individuals.

Cylindrotoma splendens Doane

The life history of the species *Cylindrotoma splendens* has been worked out in considerable detail by Dr. A. E. Cameron, from material obtained near Westholme, Vancouver Island, British Columbia, in late April, 1917. The following account is abstracted from Cameron's detailed paper (1918) on this interesting crane-fly:

The adults first appear on the wing about the middle of May. Without food they do not live longer than five or six days, but in breeding cages, where they were supplied with food in the nature of a sugar solution, they lived as long as from seven to nine days. In nature the adults were found on the wing during a period of about three weeks.

Soon after emergence the adults begin to copulate, and one male may have intercourse with more than one female. Copulation often takes place in a vertical position, the female above, the male below, with the tips of the abdomens interlocked. At times the female was noted hanging to the roof of the breeding cages, with the male suspended head downward, his body at an angle of 90° to that of the female, and his legs unsupported. If disturbed, the female may walk off, dragging her mate after her, or she may take flight, bearing the male with her. In nature the act of copulation is generally undertaken in the deep shade of the large leaves of the insect's food plants, the sexes resting on the under surface of the leaves or on the stems. Copulation may last but a few minutes or may require several hours.

The eggs are of a dull glistening white, elongate-oval in shape. Under natural conditions they are almost invariably found on the under surface of the leaves of the food plant *Trautvetteria grandis* Nuttall (Ranunculaceae), inserted beneath the incised epidermis. They

are usually deposited in series along and just within the margin of the serrate, palmately-lobed leaf. They are found in groups of one or more, all arranged parallel to one another and with their long axes perpendicular, or nearly so, to the margin of the leaf. The eggs are only partly hidden beneath the epidermis, being exposed dorsally, the margins of the slit overlapping the egg laterally and, to a lesser degree, both anteriorly and posteriorly. This arrangement of the eggs in series gives to the leaf margin a somewhat beaded appearance. When the eggs are older, the leaf margin turns brown and the presence of the eggs is readily detected. In ovipositing, the female rests on the under side of the leaf, with the tip of the abdomen directed toward the leaf edge. The abdomen is slightly flexed ventrally, and the margin of the leaf is held between the bifurcated valves of the ovipositor, which is applied to the upper surface of the leaf, while the paired cutting valves, with their blades, are applied against the under surface. These blades are then moved to and fro, cutting a slit in the epidermis. The eggs are then deposited. In no case do the eggs actually touch one another on the leaf. In the breeding cages females lay their eggs indiscriminately on both the upper and the lower surface of the leaves. In some cases, when a leaf has been eaten earlier in the season by larvae, the female will deposit her eggs along the ragged edge of this damaged part.

The indoor duration of the egg stage is from fourteen to eighteen days, but in the field as long a period as three weeks may be required. When first deposited the egg is translucent, grayish white, and spindle-shaped, with the chorion unornamented, and measures on an average 0.84 by 0.303 millimeter.

The larva requires about three hours to emerge from the egg. The chorion of the egg splits longitudinally down the mid-dorsal line, the slit extending almost half the length of the egg. In emerging, the almost transparent, grayish white larva utilizes the body tubercles as levers in freeing itself from the eggshell. As soon as it is freed from the shell, the newly hatched larva begins to feed on the leaf tissue of the host plant.

The first-stage larvae are grayish white in color, are translucent, and measure 1.19 by 0.37 millimeter in size. They feed on both the upper and the lower surface of the leaf, burrowing thru the epidermal layer with their mandibles and feeding on the parenchymatous tissue within. The young larvae are very sluggish and are not readily disturbed when feeding, the mandibles being firmly embedded in the leaf tissue. While engaged in feeding they assume various positions on the leaf surface. At the end of nine days the larvae have increased in length to 5.84 millimeters, and show all the characteristic behavior of the full-grown larvae. Growth is very slow, and before the first molt the larvae become covered with particles of their excrement, which adheres readily to the skin. The first larval molt occurs after a period of from eighteen to twenty-one days; in some cases, however, it does not occur until five or six weeks have elapsed.

The second-stage larvae gradually assume a leaf-green color as they continue to feed. Toward the end of July, coincident with the dying-off of their food plant, the larvae, which have now reached a length of from 8.32 to 9 millimeters, become quiescent and cease to feed. Feeding and movement gradually cease completely and the larvae remain clinging motionless to the leaves. As the leaves wither, the larvae drop off, and, in some cases, attach themselves to the stems; under natural conditions, however, they usually fall among the dead leaves on the ground and under these they pass the winter in a dormant condition. Many of these larvae match the brown color of the dead leaves, but some of them retain their leaf-green tint.

The overwintering larvae first show signs of activity in March of the following spring, when *Trautvetteria grandis* sends up its new shoots. Growth then proceeds rapidly until pupation in the middle of May. There seems to be one molt before hibernation and two after, the last being the casting of the larval skin, previous to pupation. The fully grown larvae measure 17 millimeters. They are invariably found on the upper surface of the leaf, and in the spring are actively engaged in feeding. On a fresh leaf the larvae usually begin by skeletonizing it, leaving the lower epidermis intact. Later on, however, large holes may be eaten completely thru the leaf. The fully grown larvae, and to a somewhat lesser degree the younger larvae, progress by a looping motion, which may be aptly compared to that

of the measuring worms (Geometridae), progression being accomplished by the aid of the mandibles and the ventral tubercles, or pseudopodia. In a quiescent condition the thoracic region of the body has a noticeable humped appearance. The fully grown larvae are very sluggish and inactive. When disturbed they relax their hold on the leaf surface and fall to the ground. Altho several hundred adults were reared, not a single parasite was discovered.

Before pupation the larva attaches itself firmly to the surface of the leaf or to the leaf petiole, by means of its anal pseudopodia. The skin splits transversely behind but is only partially sloughed off. The head, the thorax, and the first four abdominal segments of the pupa are exposed, but the apex of the abdomen remains encased in the larval skin, the terminal part of which, collapsed and wrinkled, is attached to the leaf surface. Pupation may take place on either the upper or the lower surface, but it occurs oftener on the former. If pupation takes place on the petiole, it is generally at the axil. In the breeding cages the duration of the pupal period was found to vary from six to ten days.

When the adult first emerges it is of a pale green color, which is gradually replaced by the black and yellow of the fully colored insect. From one and one-half to two hours are required for the adult to emerge. After emergence is completed, the fly rests for a short period until the cuticle hardens and the wings expand. It seems that the adherence of the larval skin to the pupa is necessary for the emergence of the adult, at least in many cases. There appears to be a large disproportion of females over males, this sometimes being as high as five to one. Since a single male may copulate with several females, this disproportion is not so serious as it appears at first sight.

LIFE ACTIVITIES OF CRANE-FLIES

The adult

Emergence.— Emergence from the pupal hull may require but a few seconds (as described for Gnophomyia by Hyslop *in litt.*, the whole operation requiring but eight seconds), or it may take several hours. The emergence of the strictly aquatic genus Antocha has not been observed, but it must be practically instantaneous as in Blepharocera and the lotic caddice flies.

Mating.— In several widely different species, the females as they emerge from the pupal hulls are at once seized in copulation by the males altho they are still callow and uncolored. Mik (1882b:40, and 1886a) discusses this curious condition in considerable detail. In all the cases that are known to the writer — *Dicranomyia trinotata*, *Discobola caesarea*, and *Cylindrotoma distinctissima* (Mik, 1886a, the last-named also cited by Mik, 1882 b), *Liogma glabrata* (Müggenberg, 1901), *Tipula rufina* (Giard, 1895), and *Tipula ultima* (Caudell, 1913) — the abdomen of the female is elongate, flabby, and nearly colorless. In *Dicranomyia trinotata* the females scarcely have time to remove their legs from the pupal sheaths before they are seized in copulation. In other cases the males emerge before the females and wait beside the pupae for the emergence of their mates, when they at once seize them in copula. In most species of Tipula the males, when seeking the females, progress by a fluttering

motion, partly flying and partly walking, over the ground or up the trunks of trees. This habit is discussed under the account of *Tipula taughannock* (p. 1013), and has been observed in other woodland-inhabiting species of this genus — as *T. macrolabis, T. fuliginosa, T. fragilis,* and others. In *T. fragilis,* when a male comes upon a pair already in copula he passes on without interrupting them. Somewhat similar mating habits are found in some species of Dicranomyia (*D. trinotata, D. badia,* and *D. simulans*), Discobola, Antocha, Chionea, *Dactylolabis montana,* some Pediciini as Dicranota, and the Cylindrotominae.

Many crane-flies have developed swarming habits for the purpose of mating, these including representatives of most of the tribes of the Limnobiinae and a few tipuline forms. *Dicranomyia morioides* was observed by Needham (1908 a:204) swarming in vast numbers near Ithaca, New York, but here the swarms consisted only of males. Likewise, *Erioptera armata* (Needham, 1908 a:206) was found swarming near Lake Forest, Illinois; but, out of several hundred individuals captured, all except three were males. The writer has observed swarming in numerous species of Ormosia, Molophilus, Erioptera, Gonomyia, Rhabdomastix, Limnophila, Ula, Epiphragma, Eriocera, Dicranota, Rhaphidolabis, Trichocera, and other genera, and here, too, the males were always predominant. The specific data may be consulted under these various headings. The males of Dicranota swarm in rather large numbers preliminary to searching for the females, which rest quietly on the branches of neighboring shrubbery. *Limnophila ultima,* as noted at Gloversville, New York, on September 7, 1916, was swarming at half past six o'clock in the evening. The swarms here consisted of from fifty to sixty individuals and took place from ten to eighteen feet above the earth. Mating took place frequently in the air, and as soon as a pair were in copula they flew away to some point to rest, many pairs being observed hanging on a clothesline a few feet away. There were three distinct swarms, which showed little tendency to fuse altho their flight area was very close. The vast swarms of *Eriocera longicornis* and of Trichocera are mentioned or discussed elsewhere in this paper. When pairs are in copula, they readily take flight, still united, the female usually trailing the male after her; altho in a few groups, in which the male is the larger individual of the two, the situation is the opposite. Brachypremna, the familiar " weaver " of the Southern States, has a very remarkable vertical dance of several

feet in shady spots, and has been aptly termed by Johnson (1907–12 [1909]: 123) "the king of the dancing tipulids." Doubtless many interesting facts remain to be discovered concerning the dances of the tropical species of Brachypremna, Tanypremna, and Megistocera.

Dancing.— The dances of *Thrypticomyia saltens* (Dol.) should be mentioned at this point. According to Doleschall (1857), Jacobson (De Meijere, 1911: 22–23), and others, this species is common in Java in shady places thruout the year. The insects have the habit of clinging to spider webs by means of the fore feet, or, if a fore foot is lacking, one of the middle legs is used. Often twenty or more of these flies are seen hanging close beside one another on a horizontally spun web, all seesawing rapidly up and down and at the same time swaying to and fro, sometimes rhythmically, sometimes not. This ludicrous tight-rope dance is continued for a long time. Somewhat similar habits have been described for *Trentepohlia pennipes*, *Rhamphidia venustissima* Alex., and other species with white tarsi.

Bobbing.— Species of Dicranomyia and Geranomyia, as well as a few other crane-flies, have the curious habit of bobbing up and down while resting, the long, slender legs acting as springs. The species of the latter genus practice this same oscillating movement while resting on a head of flowers and feeding. H. K. Munro has recorded this bobbing habit in a species of Trentepohlia (p. 943).

Resting habits.— When at rest crane-flies assume various positions which are often fairly characteristic. Many species (Erioptera, Molophilus, and some Dicranomyia) resemble spiders when flattened against a tree trunk or some other vertical support. Styringomyia resembles a bit of cobweb, the fore and middle legs stretched out in front, the hind legs directed backward. In a position of rest the tipuline forms generally hold their wings outspread or divaricate, exceptions being in the genera Longurio, Oropeza, and others, and in a few species of Tipula, as *T. arctica* and the woodland-inhabiting species of the *marmorata* group (*T. fragilis* and *T. ignobilis*). The limnobiine forms usually fold the wings incumbent over the abdomen, but here again exceptions are found in Pedicia, *Limnophila toxoneura*, and other species, which normally rest with the wings outspread. Oropeza hangs to the roofs of bridges, culverts, and similar places, with only the fore legs attached to the support, the middle legs divergent, the posterior legs hanging loosely behind. The apparently

closely allied Dolichopeza, on the contrary, has the four anterior legs on the support, the hind legs dangling, the wings divaricate. Many of these species — as Oropeza, Dolichopeza, *Dicranomyia badia*, and exotic species of the genera Thrypticomyia and Trentepohlia — habitually rest on spider webs (page 982; also, Knab, 1912). During heavy rains, crane-flies rest on the lower side of the broad leaves of deciduous trees or hide beneath loose flakes of bark.

Feeding.— The adult flies feed but little, the majority of the species whose habits are at all known merely lapping nectar from open flowers. Knuth (1909:579) and Wahlgren (1917) record the plants frequented by a number of European Tipulinae as well as by Ptychoptera. These species are found on Umbelliferae (Aegopodium, Anthriscus, Heracleum, Carum, Anethum, and other genera), on Rosaceae (Spiraea, Rubus, and other genera), and on a few other plants. A few of the local Limnobiinae have the rostrum very greatly elongated — an obvious adaptation for sucking the nectar from tubular flowers. The species of Geranomyia feed on various composite, umbelliferous, and lauraceous flowers. Toxorhina frequents composite, rhamnaceous, apocynaceous, and ericaceous plants. The exact plants frequented are discussed under the descriptions of the respective genera.

Oviposition.— The females lay their eggs in the habitat frequented by the larvae. In the case of aquatic forms — as Antocha, Hexatoma, Eriocera, and other genera — the eggs are deposited in dipping down to the water surface, one or more eggs being deposited at each descent. Forms that live in mud or moist earth lay their eggs in these situations. Many species with acute ovipositors insert the eggs carefully into the soil or other substance. The oviposition of *Limnophila* (*Eutonia*) *alleni* as noted by the writer may be regarded as typical of this class of species:

Observations made at Gloversville, New York, June 28, 1916. A female was noted ovipositing in low, wet spots along a small woodland stream. She flew about slowly and silently, just skimming the ground, until a place suitable for egg-laying was found. She finally chose a much-decayed log and the eggs were driven home securely by the acicular tergal valves of the ovipositor. Much effort is expended to place the eggs firmly and the rate of oviposition is not more than eight or ten a minute, the female often pausing to rest for several seconds. While thus engaged, the fly is entirely unconcerned with other agencies and may be picked up by hand.

The females of most crane-flies usually live but a short time after egg-laying is completed. Indeed, the entire duration of life of the adult crane-flies is probably but a few weeks at the most.

The specialized methods of oviposition in the Cylindrotominae have already been discussed on page 709 under the account of *Cylindrotoma splendens*. The species of Tipula and other genera the females of which have blunt valves to the ovipositor (Styringomyia, Macromastix, and others), all probably scatter their eggs promiscuously or else have a specialized method of egg-laying. Similarly, the species of Tipula of the *arctica* group, in which the dorsal valves of the ovipositor are very large, placed horizontally, and with the margin finely serrated, undoubtedly have a peculiar method of oviposition, but this has not yet been observed.

The egg

The number of eggs laid by crane-flies varies from about forty-five in Styringomyia to some two thousand in the larger species of Eriocera. The following table indicates the general range in the group:

Species	Number of eggs laid			Reference
	Maximum	Minimum	Average	
Ptychoptera albimana	587	520	554	Topsent, 1914–16
Styringomyia didyma	45	....	45	Terry ms.
Eriocera longicornis	1,034	872	952	Alexander ms.
spinosa	2,061	1,824	1,942	Alexander ms.
Hexatoma megacera	372	316	347	Alexander, 1915 c
Phalacrocera replicata	60	....	60	Miall and Shelford, 1897
Liogma glabrata	60	....	60	Müggenberg, 1901
Ctenophora angustipennis	400	200	300	Lovett, 1915
Tipula cunctans	....	....	300	Hyslop, 1910
bicornis	297	282	289	Webster, 1893 b
tephrocephala	255	....	255	Webster, 1893 b
angustipennis	602	....	602	Hyslop, 1910
collaris	329	....	329	Alexander ms.
dejecta	366	251	309	Alexander ms.
oleracea	600	....	600	Del Guercio, 1914

The eggs are in most cases elongate with the ends narrowed and rounded, or, in other words, spindle-shaped. The chorion in the species of Tipula, Hexatoma, and other genera is blackened and in some cases more or less sculptured. In *Ctenophora angustipennis* (Lovett, 1915) the egg is ebony black with deep purple reflection, elongate-oval, uniform, without pits or ridges, and measuring from 1.26 to 1.4 millimeters by 0.375 millimeter.

In *Tipula bicornis* (Webster, 1893 b) the egg is 0.8 millimeter long by 0.3 to 0.4 millimeter in diameter, elongate-ovoid, with one side deeply concave, the surface highly polished. The egg of *Nephrotoma ferruginea* is smaller, with five distinct grooves. The egg of *Tipula glacialis* (Pokorny, 1887:53) is described as being 1.2 millimeters long and only 0.3 millimeter in diameter, cylindrical, the two ends equally rounded, the surface smooth, shiny black, with faint steel-blue or purplish red reflections. In many other genera of Tipulidae, especially the smaller forms, the eggs are soft and whitish or nearly hyaline. In a few species the eggs take on a decided green or greenish tinge. The egg of *Cylindrotoma splendens* is described elsewhere in this paper (page 709). The egg of *Ptychoptera albimana*, as described by Topsent (1914–16), measures 0.825 by 0.264 millimeter, and is pale yellow, slightly arcuated, and with the surface curiously ornamented.

The larva

As a rule, the larvae live in the haunts where the eggs are laid. The duration of the larval stage varies from about a month in Styringomyia (larva and pupa together, thirty-seven days — Terry ms.) to the greater part of a year in most crane-flies. Many of the smaller species of Erioptera, Ormosia, Rhaphidolabis, and other genera are on the wing in the spring and again in the fall, and with little doubt are double-brooded. This would make the larval existence but a few months, but still probably longer than the other stages taken together. This problem of double broods should be worked out carefully. It often appears that there are two broods, when in reality there may be two developing generations, each passing the winter as larvae, but one attaining its growth much more slowly in the spring and summer and not maturing until late summer. Phalacrocera and *Cylindrotoma splendens* spend about eleven months in the larval stage (Bengtsson 1897, and Cameron 1918), while *Tipula paludosa* spends nine months in that stage (Rennie, 1917). It is probable that nearly all crane-flies in the North Temperate Zone winter normally as larvae. The growth during summer, fall, and winter is very slight, but in the spring it is greatly accelerated and in a month the larva may attain its full growth. Larvae of *Tipula ignobilis* taken at Ithaca, New York, on April 23, 1917, measured only 6.5 millimeters in length; on May 19 they had attained their full growth of 18 millimeters and were ready to pupate. *Cylindrotoma splendens* spends the winter as a larva,

9 millimeters in length, but grows rapidly during the spring, attaining its full size (17 millimeters) in two months of growth. *Liogma glabrata* spends the winter as a very small larva, but in the spring its growth is greatly accelerated.

The haunts in which the larvae of crane-flies occur are exceedingly varied. In the case of single large genera, such as Dicranomyia and Tipula, the species range from those that are almost strictly aquatic to others that are entirely terrestrial, living in decaying wood or even mining in the leaves of plants.

The transition between strictly aquatic and terrestrial forms is very gradual, as was pointed out by Miall (1895:11) some years ago when he wrote:

> How did insects ever come to seek the water, seeing that their mode of respiration is primarily adapted to another element? We can see almost all the steps of the adaptation on the shores of our rivers, lakes and seas. We can see dipterous larvae which, like the "leather jacket" (the larva of the daddy-long-legs), burrow in the ground for their vegetable food, and devour the roots of grasses. Other larvae of the same family (Tipulidae) prefer moist earth in the neighborhood of streams. Others again live immersed in water, or mud saturated with water, though they come to the surface at times and push their tails, which carry the spiracles, into the air. Some few have become so completely aquatic that they seldom, if ever, come to the surface, and all their supply of oxygen is obtained from the water.

The culmination of this latter condition is reached in forms such as Antocha and related genera and species. Crampton (1919:100) has made similar observations on the subject.

The haunts of the larvae of crane-flies are best shown by the following table, in which the various species are arranged according to habitat, from the strictly aquatic to the various terrestrial forms:

Habitat	Species
Strictly aquatic, in silken cases	Antocha
In very rapid water (lotic) on or in submerged mosses (hygropetric association)	*Dicranomyia simulans*, Pedicia, Triogma, Tipuline No. 1, and others
Aquatic, on submerged plants	Phalacrocera, Triogma
Semi-aquatic (part of life spent in water, but pupation taking place on land)	*Dicranomyia simulans*, Eriocera, Hexatoma, Aeshnasoma, Longurio, *Tipula abdominalis*, *T. caloptera*, *T. bella*, and others
On cliffs and wooden walls, usually in silken cases covered by water	*Dicranomyia simulans*, Geranomyia, Elliptera, Dactylolabis, and others
In cold springs	Pedicia, Thaumastoptera

Habitat	Species
In stagnant water in the axils of bromeliaceous and other plants	Trentepohlia, *Gnophomyia rufa*
Amphibious in decaying wood	Protoplasa (supposition), Epiphragma
In mud or sand:	
a. In open swamps	Bittacomorpha, Ptychoptera, Rhamphidia, *Erioptera septemtrionis, E. chlorophylla, E. vespertina, Limnophila adusta, L. macrocera, Pilaria recondita, P. tenuipes, P. quadrata, Tricyphona inconstans*, Prionocera, *Tipula dejecta, T. sayi, T. tricolor*, and others
b. In shaded woods	Bittacomorphella, *Ormosia innocens, Erioptera megophthalma, Molophilus hirtipennis*, Ulomorpha, Dicranophragma, Penthoptera, *Tipula cayuga*, and others
c. Along the margins of streams and other bodies of water	*Limnobia fallax, Erioptera (Hoplolabis) armata*, Trimicra, *Gonomyia (Leiponeura) alexanderi, G. kansensis*, Eriocera, Hexatoma, and others
In or beneath damp cushions of moss	*Dicranomyia badia, D. stulta, Tipula oropezoides, T. collaris, T. nobilis, T. ignobilis*, and others
In or beneath dry cushions of moss	Liogma, Dolichopeza, Oropeza, and others
In dry soil	Dicranoptycha, Cladura, *Nephrotoma ferruginea, Tipula cunctans, T. angustipennis*, and others
In fungi	*Limnobia triocellata, L. cinctipes*, Ula, and others
In decaying vegetables, plant stems, manure, and like situations	Trichocera, *Limnobia indigena, Rhipidia domestica, R. maculata*, and others
In wood:	
a. In decaying wood, usually just beneath the bark	*Dicranomyia rara, D. macateei, Rhipidia fidelis, R. bryanti*, Elephantomyia, Teucholabis, Gnophomyia, *Limnophila unica*, Brachypremna, Ctenophora, Dictenidia, *Tipula trivittata, T. usitata*, and others
b. In nearly solid wood	Tanyptera
On leaves of terrestrial plants:	
a. On flowering plants	Cylindrotoma
b. On mosses	Liogma, Triogma (in some instances)
Mining in the leaves of plants	*Dicranomyia foliocuniculator*

Feeding.— The various larvae of crane-flies show a considerable diversity in their habits of feeding. The majority of species, as known, are herbivorous, but a large group are decidedly carnivorous in their habits.

The Tipulinae feed on the living vegetable tissue or plant remains occurring in their habitat, or, when pressed for food, they will eat earth-

worms (Patterson, 1908) and other soft-bodied animals. Dissections of *Tipula abdominalis* show the food of this species to consist principally of small filamentous algae, diatoms (Diatoma, Navicula, and others), and rootlets of small plants. The alimentary tract is often crammed with sand or soil particles. The species of Tipula and Nephrotoma that are injurious to plants, considered later in this paper under the heading *Economic Importance*, effect their damage by devouring the living tissues of the roots. The Cylindrotominae feed on the living tissues of the plants on which they dwell; in the case of Phalacrocera, Triogma, and Liogma these are mosses, in Cylindrotoma they are the parenchyma and epidermis of higher plants (spermatophytes). With this habit of feeding on plant tissues the extreme of sluggishness of motion is attained. The wood-boring species of Tipulinae (such as the species of Tanyptera and Ctenophora) feed on the ligneous tissue of the trees in which they occur. Other species of crane-flies injure young seedlings by destroying the bark and the bast tissues.

The hexatomine and pediciine forms represent the opposite extreme, being for the most part carnivorous or even cannibalistic in their habits. In order to capture their prey they are of necessity rapid of movement, and in this group the most graceful and active of all tipulid larvae are found. The motions of the species are, at times, exceedingly agile and snakelike. The food consists of a variety of animal forms. Dicranota has been recorded as feeding on worms of the genus Tubifex. Pedicia usually feeds on the larvae of small insects, especially Chironomidae, but the large species of this genus and of Eriocera are capable of capturing almost any insect of a size equal to their own. The larvae of *Eriocera spinosa* are able to inflict painful bites on tender parts of the skin of a man. Penthoptera, Eriocera, Hexatoma, and most of the limnophiline groups likewise feed largely on midge larvae. From one small larva of *Limnophila* (*Dicranophragma*) *fuscovaria* the writer has dissected out the remains of two large midge larvae, whose heads were nearly half the size of that of the captor. The chitinized mentum in these predacious forms is very weak or is lacking, allowing for a tremendous distension of the gular region. The mandibles are always developed into powerful curved hooks which serve well their purpose of grasping and holding the victims. The esophageal region is often retrorsely roughened to prevent the egress of anything that has once started down the throat. In addition to the

various chitinized jaws, legs, heads, and other insect remains, the distended proventricular regions usually show a considerable amount of sand particles and much plant tissue.

The pupa

When ready to pupate, the larva ceases feeding and becomes much contracted and sluggish. The pupa is formed within the last larval skin, which is then shed completely except in certain Cylindrotominae and a few scattered genera in other tribes, in which cases the larval skin adheres to the posterior end of the abdomen. The pupal existence is spent in or near the haunts of the larva.

In the strictly aquatic genus Antocha the pupa lives in water in a silken case, respiration being accomplished by means of the many-branched breathing horns. The species of Elliptera and certain Dicranomyia (*simulans*, for example) approach this aquatic condition. The other species of crane-flies with aquatic larvae known to the writer go to the soil in order to pupate, this category including Eriocera, Hexatoma, *Tipula caloptera*, *T. abdominalis*, and many others.

The pupae of some, at least, of the Cylindrotominae attach themselves to plant stems for the purpose of pupation. The leaf-mining *Dicranomyia foliocuniculator* pupates within the larval passages. The majority of the limnobiine forms spend the pupal existence in silken cases to which pebbles and particles of débris or plant tissues adhere.

The pupae of the Ptychopteridae have one of the two breathing horns enormously elongated, the tip of this being projected above the water level into the air for respiration. Certain tipuline crane-flies have a somewhat similar development of the breathing horns, discussed later.

The duration of the pupal existence is remarkably uniform thruout the group, averaging from six to eight days. The following table illustrates this for the more representative genera and species. Records which have not been determined sufficiently close, and which as stated are probably too long, are indicated by an asterisk.

Species	Duration of pupal existence (days)			Reference
	Maximum	Minimum	Average	
Ptychoptera rufocincta	....	$4\frac{3}{4}$	....	Alexander ms.
albimana	*12	10	11	Topsent, 1914–16
Bittacomorphella	*13	....	....	Alexander ms.
Dicranomyia badia	7	....	7	Alexander ms.
stulta	*8	....	....	Alexander ms.
Rhipidia bryanti	7	....	7	Shannon ms.
Limnobia cinctipes	....	5	....	Alexander ms.
triocellata	9	8	$8\frac{1}{2}$	Alexander ms.
Rhamphidia mainensis	6	....	6	Alexander ms.
Dicranoptycha winnemana	*10	....	....	Alexander ms.
Ula elegans	*10	....	....	Alexander, 1915a
Epiphragma	....	6	6	Alexander ms.
Pseudolimnophila	9	8	$8\frac{1}{2}$	Alexander ms.
Limnophila macrocera	9	8	$8\frac{1}{2}$	Alexander ms.
fuscovaria	*14	8	10	Alexander ms.
Pilaria	7	7	7	Alexander ms.
Ulomorpha	*9	....	....	Alexander ms.
Eriocera fultonensis	7	7	7	Alexander ms.
longicornis	7.3	....	7.3	Alexander ms.
Hexatoma megacera	$6\frac{1}{2}$	....	$6\frac{1}{2}$	Alexander ms.
Pedicia rivosa	*14	7	$10\frac{1}{2}$	Beling, 1879:46
Erioptera macrophthalma	8	7	$7\frac{1}{2}$	Alexander ms.
Molophilus hirtipennis	*10	....	....	Alexander ms.
Gnophomyia tristissima	5	4	$4\frac{1}{2}$	Hyslop ms.
Ormosia nigripila	*11	....	....	Alexander ms.
Teucholabis complexa	9	....	......	Johnson ms.
Elephantomyia	8	6	7	Shannon ms.
Cylindrotoma splendens	10	6	8	Cameron, 1918
Liogma glabrata	11	10	$10\frac{1}{2}$	Müggenberg, 1901
Phalacrocera replicata	8	7	$7\frac{1}{2}$	Bengtsson, 1897
Dolichopeza albipes	6	....	6	Beling, 1886 (as *sylvicola*)
Ctenophora angustipennis	....	....	10	Lovett, 1915
Dictenidia bimaculata	7	....	7	Beling, 1873b
Tipula maxima	*14	*10	*12	Beling, 1886
oleracea	8	7	$7\frac{1}{2}$	Del Guercio, 1914:315
cayuga	7.6	....	7.6	Alexander ms.
ignobilis	8	7	$7\frac{1}{2}$	Alexander ms.
dejecta	8	....	8	Alexander ms.
collaris	8	7	$7\frac{1}{2}$	Alexander ms.
Nephrotoma lineata	7	....	7	Beling, 1879 (as *histrio*)
lunulicornis	7	....	7	Beling, 1879
analis	*12	*8	*10	Beling, 1886

ENEMIES

Crane-flies have many enemies and but few means of combating them. Every stage of the crane-fly's existence is fraught with danger. The larvae of the majority of species are soft-bodied, herbivorous creatures, which form a choice morsel of food for carnivorous forms of many classes and orders. The period when the adult fly has just emerged from the pupal hull is undoubtedly the one in which the greatest danger is found, for then the insects are teneral and incapable of rapid motion. The adult flies are sometimes drowned in the sea or other large bodies of water and their dead fragments cast up in windrows on the shore. A very unusual instance of this kind is recorded for *Tipula oleracea* by Patterson (1908). At their best, the adult flies are poor, awkward fliers and are easily captured by a wide range of species, as indicated in the following pages.

Predatory natural enemies

Vertebrates

Mammalia.— Undoubtedly many of the smaller mammals prey on the larvae of various species of Tipula. In another paper (Alexander, 1919 d: 776–777) the writer has discussed the value of the larvae of an undetermined species of Tipula in the Pribilof Islands as an article of food for the arctic fox. These larvae occur in enormous numbers beneath the lichens of the tundra and the foxes can easily get them at a time when other food is scarce or unobtainable. Mice, shrews, and moles find an important element of their food from this source. White (1914) states that in North Wales the European mole, *Talpa europaea*, eats, on an average, twenty crane-fly larvae a day, these constituting one of the main foods of this mammal.

Aves.— Birds are well-known enemies of crane-flies, both in their immature stages and as adult flies. Hyslop (1910: 129–130) lists ninety-one species of birds which are known to feed on crane-flies. Baer (1913) describes ravens and starlings as feeding on the larvae of a species of Tipula. While working with the United States Biological Survey, the writer was given the opportunity to examine files for records. His thanks for assistance in this work are due to Messrs. Kalmbach, McAtee, and Wetmore. The records of the Survey are based on an examination of the contents of the stomachs of many thousands of individuals, and furnish very valuable and fairly complete data on the North American

birds which prey on various stages of the Tipulidae. These records are here arranged according to the latest check list of the American Ornithologists' Union:[3]

Longipennes:
- Laridae:
  - *Larus delawarensis* Ord. Ring-billed gull
  - *L. franklinii* Rich. Franklin's gull
  - *Sterna hirundo* Linn. Common tern

Anseres:
- Anatidae:
  - *Mergus americanus* Cass. Merganser
  - *Anas platyrhynchos* Linn. Mallard
  - *A. rubripes* Brewst. Black duck
  - *Mareca americana* (Gmel.). Baldpate
  - *Nettion carolinense* (Gmel.). Green-winged teal
  - *Dafila acuta* (Linn.). Pintail
  - *Aix sponsa* (Linn.). Wood duck

Herodiones:
- Ardeidae:
  - *Egretta candidissima candidissima* (Gmel.). Snowy egret
  - *Butorides virescens virescens* (Linn.). Green heron

Limicolae:
- Phalaropodidae:
  - *Phalaropus fulicarius* (Linn.). Red phalarope
  - *Lobipes lobatus* (Linn.). Northern phalarope
  - *Steganopus tricolor* Vieill. Wilson's phalarope
- Recurvirostridae:
  - *Recurvirostra americana* Gmel. Avocet
  - *Himantopus mexicanus* (Müll.). Black-necked stilt
- Scolopacidae:
  - *Philohela minor* (Gmel.). American woodcock
  - *Gallinago delicata* (Ord). Wilson's snipe
  - *Arquatella maritima maritima* (Brünn.). Purple sandpiper
  - *Pisobia aurita* (Lath.). Sharp-tailed sandpiper
  - *P. maculata* (Vieill.). Pectoral sandpiper
  - *P. bairdii* (Coues). Baird's sandpiper
  - *Limosa fedoa* (Linn.). Marbled godwit
  - *Totanus flavipes* (Gmel.). Yellow-legs
  - *Heteractitis incanus* (Gmel.). Wandering tatler
  - *Bartramia longicauda* (Bechst.). Bartramian sandpiper
- Charadriidae:
  - *Charadrius dominicus dominicus* (Müll.). Golden plover
  - *Oxyechus vociferus* (Linn.). Killdeer
- Aphrizidae:
  - *Arenaria interpres interpres* (Linn.). Turnstone

Gallinae:
- Tetraonidae:
  - *Bonasa umbellus umbellus* (Linn.). Ruffed grouse

Raptores:
- Buteonidae:
  - *Ictinia mississippiensis* (Wils.). Mississippi kite

[3] Check list of North American birds, 3d ed., p. 1-430. American Ornithologists' Union. 1910.

Coccyges:
- Cuculidae:
  - *Coccyzus americanus americanus* (Linn.). Yellow-billed cuckoo
  - *C. erythrophthalmus* (Wils.). Black-billed cuckoo
  - *Cuculus canorus telephonus* Heine. Kamchatka cuckoo

Pici:
- Picidae:
  - *Dryobates pubescens pubescens* (Linn.). Downy woodpecker
  - *D. nuttalii* (Gamb.). Nuttall's woodpecker
  - *Sphyrapicus varius varius* (Linn.). Yellow-bellied sapsucker
  - *S. thyroideus* (Cass.). Williamson's sapsucker
  - *Melanerpes erythrocephalus* (Linn.). Red-headed woodpecker
  - *Asyndesmus lewisi* Riley. Lewis's woodpecker
  - *Colaptes auratus auratus* (Linn.). Flicker

Macrochires:
- Caprimulgidae:
  - *Antrostomus carolinensis* (Gmel.). Chuck-will's-widow
  - *Chordeiles virginianus virginianus* (Gmel.). Nighthawk
  - *C. acutipennis texensis* Lawr. Texas nighthawk
- Cypselidae:
  - *Chaetura pelagica* (Linn.). Chimney swift
  - *C. vauxi* (J. K. Towns.). Vaux's swift
  - *Aëronautes melanoleucus* (Baird). White-throated swift
- Trochilidae:
  - *Calypte anna* (Less.). Anna's humming bird
  - *Selasphorus rufus* (Gmel.). Rufous humming bird

Passeres:
- Tyrannidae:
  - *Tyrannus tyrannus* (Linn.). Kingbird
  - *T. verticalis* Say. Arkansas kingbird
  - *T. vociferans* Swains. Cassin's kingbird
  - *Myiarchus crinitus* (Linn.). Great-crested flycatcher
  - *Sayornis phoebe* (Lath.). Phoebe
  - *S. sayus* (Bonap.). Say's phoebe
  - *S. nigricans* (Swains.). Black phoebe
  - *Myiochanes virens* (Linn.). Wood pewee
  - *M. richardsonii richardsonii* (Swains.). Western wood pewee
  - *Empidonax flaviventris* (W. M. & S. F. Baird). Yellow-bellied flycatcher
  - *E. difficilis difficilis* Baird. Western flycatcher
  - *E. virescens* (Vieill.). Acadian flycatcher
  - *E. traillii traillii* (Aud.). Traill's flycatcher
  - *E. minimus* (W. M. & S. F. Baird). Least flycatcher
  - *E. wrightii* Baird. Wright's flycatcher
  - *E. griseus* Brewst. Gray flycatcher
- Corvidae:
  - *Pica pica hudsonia* (Sab.). American magpie
  - *Cyanocitta cristata cristata* (Linn.). Blue jay
  - *C. stelleri stelleri* (Gmel.). Steller's jay
  - *Corvus brachyrhynchos brachyrhynchos* Brehm. American crow
  - *C. ossifragus* Wils. Fish crow
- Sturnidae:
  - *Sturnus vulgaris* Linn. Starling
- Icteridae:
  - *Dolichonyx oryzivorus* (Linn.). Bobolink
  - *Molothrus ater ater* (Bodd.). Cowbird

Passeres (*continued*):
Icteridae (*continued*):
Xanthocephalus xanthocephalus (Bonap.). Yellow-headed blackbird
Agelaius phoeniceus phoeniceus (Linn.). Red-winged blackbird
A. gubernator californicus Nels. Bicolored redwing
Sturnella magna magna (Linn.). Meadow lark
Icterus spurius (Linn.). Orchard oriole
I. galbula (Linn.). Baltimore oriole
I. bullockii (Swains.). Bullock's oriole
Euphagus cyanocephalus (Wagl.). Brewer's blackbird
Quiscalus quiscula quiscula (Linn.). Purple grackle
Fringillidae:
Leucosticte griseonucha (Brandt). Aleutian rosy finch
Plectrophenax nivalis nivalis (Linn.). Snow bunting
P. hyperboreus Ridgw. McKay's snow bunting
Calcarius lapponicus lapponicus (Linn.). Lapland longspur
Passerculus sandwichensis savanna (Wils.). Savanna sparrow
Zonotrichia leucophrys leucophrys (J. R. Forst.). White-crowned sparrow
Z. albicollis (Gmel.). White-throated sparrow
Junco hyemalis hyemalis (Linn.). Slate-colored junco
Passer domesticus (Linn.). English sparrow
Melospiza melodia melodia (Wils.). Song sparrow
M. lincolnii lincolnii (Aud.). Lincoln's sparrow
M. georgiana (Lath.). Swamp sparrow
Passerella iliaca iliaca (Merr.). Fox sparrow
Pipilo erythrophthalmus erythrophthalmus (Linn.). Towhee
Passerina amoena (Say). Lazuli bunting
Tangaridae:
Piranga ludoviciana (Wils.). Western tanager
P. erythromelas (Vieill.). Scarlet tanager
P. rubra rubra (Linn.). Summer tanager
Hirundinidae:
Progne subis subis (Linn.). Purple martin
Petrochelidon lunifrons lunifrons (Say). Cliff swallow
Hirundo erythrogastra Bodd. Barn swallow
Iridoprocne bicolor (Vieill.). Tree swallow
Tachycineta thalassina lepida Mearns. Northern violet-green swallow
Riparia riparia (Linn.). Bank swallow
Stelgidopteryx serripennis (Aud.). Rough-winged swallow
Bombycillidae:
Bombycilla cedrorum Vieill. Cedar waxwing
Vireonidae:
Vireosylva olivacea (Linn.). Red-eyed vireo
V. philadelphica (Cass.). Philadelphia vireo
V. gilva gilva (Vieill.). Warbling vireo
Lanivireo solitarius solitarius (Wils.). Blue-headed vireo
Vireo griseus griseus (Bodd.). White-eyed vireo
V. bellii bellii Aud. Bell's vireo
V. bellii pusillus Coues. Least vireo
Mniotiltidae:
Mniotilta varia (Linn.). Black-and-white warbler
Helmitheros vermivorus (Gmel.). Worm-eating warbler
Dendroica aestiva aestiva (Gmel.). Yellow warbler
D. coronata (Linn.). Myrtle warbler
D. auduboni auduboni (Towns.). Audubon's warbler

Passeres (*continued*):
  Mniotiltidae (*continued*):
    D. dominica dominica (Linn.). Yellow-throated warbler
    Oporornis tolmiei (J. K. Towns.). Macgillivray's warbler
    Geothlypis trichas trichas (Linn.). Maryland yellowthroat
    Icteria virens virens (Linn.). Yellow-breasted chat
    Wilsonia pusilla pusilla (Wils.). Wilson's warbler
    Setophaga ruticilla (Linn.). American redstart
  Motacillidae:
    Anthus rubescens (Tunst.). Pipit
  Mimidae:
    Mimus polyglottos polyglottos (Linn.). Mocking bird
    Dumetella carolinensis (Linn.). Catbird
    Toxostoma rufum (Linn.). Brown thrasher
    T. redivivum (Gamb.). Californian thrasher
  Troglodytidae:
    Heleodytes brunneicapillus couesi (Sharpe). Cactus wren
    Salpinctes obsoletus obsoletus (Say). Rock wren
    Catherpes mexicanus punctulatus Ridgw. Dotted canon wren
    Thryothorus ludovicianus ludovicianus (Lath.). Carolina wren
    Thryomanes bewickii bewickii (Aud.). Bewick's wren
    Nannus hiemalis hiemalis (Vieill.). Winter wren
    Telmatodytes palustris palustris (Wils.). Long-billed marsh wren
  Paridae:
    Baeolophus inornatus inornatus (Gamb.). Plain titmouse
    Penthestes atricapillus atricapillus (Linn.). Chickadee
    P. carolinensis carolinensis (Aud.). Carolina chickadee
    P. gambeli gambeli (Ridgw.). Mountain chickadee
    P. hudsonicus hudsonicus (Forst.). Hudsonian chickadee
    Psaltriparus minimus minimus (J. K. Towns.). Bush-tit
  Chamaeidae:
    Chamaea fasciata fasciata (Gamb.). Wren-tit
  Sylviidae:
    Regulus calendula calendula (Linn.). Ruby-crowned kinglet
  Turdidae:
    Myadestes townsendi (Aud.). Townsend's solitaire
    Hylocichla mustelina (Gmel.). Wood thrush
    H. fuscescens fuscescens (Steph.). Veery
    H. aliciae aliciae (Baird). Gray-cheeked thrush
    H. ustulata ustulata (Nutt.). Russet-backed thrush
    H. ustulata swainsoni (Tschudi). Olive-backed thrush
    H. guttata pallasii (Cab.). Hermit thrush
    Planesticus migratorius migratorius (Linn.). American robin

The principal families that feed on the adult flies are the Caprimulgidae, the Cypselidae, the Tyrannidae, the Icteridae, the Hirundinidae, the Mniotiltidae, the Troglodytidae, the Paridae, and the Turdidae.

Many species of birds feed on the larvae of crane-flies, the more notable of these being the water-fowl, Anatidae, the shore birds, Scolopacidae, and the thrushes, Turdidae. Sim (1907) has recorded the chestnut-sided warbler, *Dendroica pensylvanica* (Linn.) as feeding on *Tipula* sp.

In Europe the raven and the starling are important, as already stated. Patterson (1908) records the starling as eating great numbers of *Tipula oleracea* and as boring into the soil in search of the larvae of this species.

It will be noted that in the foregoing list no species of doves or pigeons are recorded in this country as feeding on Tipulidae. The following note on an Australian pigeon shows the importance of the larvae as a food for these birds: [4]

Mr. North exhibited the head, crop, and gizzard of a wonga-wonga pigeon (*Leucosarcia picata* Lath.) shot by Mr. H. J. McCooey in a myrtle scrub at Upper Burragorang on the 21st inst. The crop is absolutely crammed with dipterous larvae (*Habromastix cinerascens* Sk.) and undigested portions of them mixed with seeds, berries, and earth appear also in the gizzard. As the larvae are known to be destructive to grass, the wonga-wonga would appear to be deserving of consideration.

Amphibia.— Crane-flies, both larvae and adults, form a considerable element of the food of many Amphibia. The studies by Needham (1905:13) show this to be true in the case of the bullfrog, *Rana catesbeiana* Shaw. Munz (1920) studied the food habits of eight species of Anura and found that five fed on crane-fly larvae or adults. These species were *Rana clamitans* Latr., *R. sylvatica* Lec., *R. palustris* Lec., *R. pipiens* Schreb., and *Hyla crucifer* Wied. The following additional records are given:

Desmognathus fusca Raf. Dusky salamander. Wings of a Limnophila found in a specimen from Ithaca, New York. (A. A. Noyes.)

Rana clamitans Latr. Green frog. Two larvae of a Tipula, near *dejecta* Walker, found in stomach. (S. W. Frost.)

Bufo lentiginosus woodhousei Girard. Centerville, Utah, April 27, 1912. Twenty-six per cent of the food of this species consisted of a large tipulid. (E. R. Kalmbach.)

Bufo sp. Washington, D. C., May 17, 1890. One per cent tipulid larvae. (W. L. McAtee.)

Pisces.— The larvae of crane-flies furnish favorite morsels for many carnivorous species of fish, and as a consequence they are in considerable demand with fishermen as bait for bass and other game fish. These include the larvae of the larger species of Eriocera and many large semiaquatic species of Tipula, especially *Tipula caloptera* and *T. abdominalis*. Fragments of the adult flies are often found in the stomach contents of fish, notably species of trout, most of these pieces being of individuals that

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[4] Linn. Soc. New South Wales. Proc., ser. 2:9:585. 1894.

had fallen into the water or were captured while newly transformed. Forbes (1888) records Coregonus and Hyodon as feeding on the eggs, and Notropis as feeding on the larvae, of crane-flies. Levander (1909:1) records *Perca fluviatilis* Linn. as feeding on larvae of Tipulidae.

Invertebrates

Arachnida. — Some spiders are notable enemies of crane-flies, which fall easy victims while in a helpless, teneral condition. These spiders represent many families, such as the Thomisidae, the Lycosidae, the Attidae, the Epeiridae, and others (Alexander and Lloyd, 1914:15; also, Alexander, 1915 c:144). An account of their preying on the larger crane-flies of the genus Tipula is given under the discussion of *T. taughannock* (page 1013). In a recent paper Bilsing (1920) has recorded four species of crane-flies eaten by spiders. These spiders represented thirteen species arranged in four families — the Lycosidae, the Attidae, the Epeiridae, and the Agelenidae. J. R. Malloch found a female *Tipula angustipennis* which was being eaten by a crab spider, determined by Mr. Banks as *Xysticus ferox* Htz. The spider did not release its hold until after it was placed in a jar of cyanide.

Hexapoda.— Odonata: The following records of dragon-flies found feeding on adult crane-flies are available: *Gomphus vastus* Walsh and *G. ventricosus* Walsh, found feeding on *Tipula bicornis* at South Bend, Indiana, May 30, 1914 (E. B. Williamson); *Helocordulia uhleri* (Selys), found feeding on *Eriocera longicornis* (Alexander, 1915c:152); *Agrion puella* Linn., found feeding on *Erioptera flavescens* (Campion, 1914:498). C. H. Kennedy has sent the writer a male and a female specimen of a small crane-fly, *Teucholabis pabulatoria* Alex., which he found in the mouth of a damsel fly, *Hetaerina tricolor* Burm., collected in Guatemala by Professor Hine. Needham and Hart (1901–03 [1901]:47) record the nymphs of *Anax junius* (Dru.) feeding on the larvae of Tipulidae.

Diptera: The adult flies of at least three families of the order Diptera — the Asilidae, the Empididae, and the Scatophagidae — and the larvae of a fourth, Anthomyiidae, are notable enemies of crane-flies. The records of Kirby (1892), Poulton (1906–07), Bromley (1914), Alexander (1915c), and McAtee and Banks (1920) on the first three of these families may be summarized as follows:

Asilidae (robber flies)	Prey
Lasiopogon cinctus (Fabr.)	*Nephrotoma lineata* (Scop.) (Poulton, 1906–07, as *histrio* [Fabr.])
Neoitamus cyanurus (Lw.) (in copulation with female, the latter with the crane-fly)	*Tipula scripta* Meig. (Poulton, 1906–07)
Proctacanthus philadelphicus Macq.	*Nephrotoma* sp. (2 records, Bromley, 1914)
Asilus sp.	*Nephrotoma ferruginea* (Fabr.) (3 records, Alexander, 1915 c)
Asilus flavofemoratus Hine	*Tipula* sp. (McAtee and Banks, 1920: 30)
Asilus notatus Wied.	*Nephrotoma ferruginea* (Fabr.) (McAtee and Banks, 1920: 31)
Asilus paropus Walk.	*Epiphragma solatrix* (O. S.) (McAtee and Banks, 1920: 31)
Asilinae	*Tipula lateralis* Meig. (Poulton, 1906–07)

The Empididae, or dance flies, are small, predacious flies which are closely related to the robber flies and largely replace them in moist shaded situations. They unquestionably play a most important part in the economy of the Tipulidae, since both groups are practically confined to the same general situations and, in the temperate regions at least, representatives of the two groups are invariably found together. Macquart (Kirby, 1892: 229), discussing *Empis livida* Linn., writes as follows: "Among the thousands of pairs which I have noticed resting on bushes or hedges, nearly all the females were engaged in sucking some insect, sometimes small Phryganidae or Ephemeridae, but more often Tipulidae. They busy themselves with feeding and perpetuating their species at the same time." Howlett (1907) records *Empis borealis* Linn. as feeding on Tipulidae. The following records are from Poulton (1906–07: 380–382): *Empis tesselata* Fabr. preys on *Tipula lunata* Linn., *T. paludosa* Meig., and other species; *Empis livida* Linn. preys on *Dicranomyia* sp. (It is probable that the long-legged flies, Dolichopodidae, likewise play an important rôle in the lives of the Tipulidae, but no records are available to the writer to confirm this belief.)

The Scatophagidae (Cordyluridae), or dung flies, unquestionably play an important part in the lives of the smaller crane-flies (Limnobiinae). The following records indicate this relationship, the last being supplied by Malloch:

Enemy	Prey
Scatophaga suilla (Fabr.)	*Dicranomyia lutea* (Meig.) (Poulton, 1906–07)
Scatophaga sp. (*stercoraria?*)	*Erioptera* sp. (Poulton, 1906–07)
Scatophaga sp.	*Hexatoma megacera* (O. S.) (Alexander, 1915 c)
Scatophaga stercoraria (L.) and *squalida* Meig.	*Trichocera* (Malloch, 1911)

Comparatively recently the larvae of Anthomyiidae have been found to play a highly important rôle in the economy of other insects living in the same haunts. The very important paper by Keilin (1917) may be consulted in connection with this point. This student found the following Anthomyiidae associated with Tipulidae: *Graphomyia maculata* Scop., feeding on larvae of *Ptychoptera contaminata* (L.) (Keilin, 1917: 354–360); *Allognota agromyzina* Fall., associated with and possibly feeding on the larvae of *Ula macroptera* Macq. (page 360–362 of reference cited); *Phaonia cincta* Zett., feeding on larvae and pupae of *Mycetobia pallipes* (page 362–375 of reference); *Phaonia goberti* Mik, associated with and possibly feeding on the larvae of *Gnophomyia tripudians* Bergr. (page

375–377 of reference); *Mydaea pertusa* Meig., possibly feeding on larvae of Tipulidae (page 393–396 of reference).

A species of Phaonia with presumably parasitic habits is discussed on page 732 of this memoir.

Coleoptera: The adults and the larvae of the following species of ground beetles (Carabidae) have been recorded as important enemies of crane-flies (Hyslop, 1910): *Poecilus lucublandus* Say; *Micromaseus femoralis* (Kirby); *Platynus* sp.; *Harpalus pennsylvanicus* Dej.; *H. caliginosus* Fabr. Most of these were recorded by Webster (1893 a:241) as feeding on the injurious crane-fly *Tipula bicornis*.

The larvae of Elateridae (wireworms) are enemies of crane-flies. The writer has seen several feeding on large larvae of *Tipula trivittata*.

Hymenoptera: Ants (Formicidae) undoubtedly capture and devour many crane-flies, these generally being pupae or teneral adults. Hyslop (1910) cites the record of an *Aphaenogaster fulva* Roger which was observed dragging a living adult tipulid over the ground. Chapman (1918:191) records feeding species of Myrmica on adult Tipulidae which were readily eaten by the ants in preference to most other insect food. On August 2, 1917, at Larned, Pawnee County, Kansas, along the bank of the Arkansas River, the writer noted a small ant which was dragging a still living pupa of *Gonomyia kansensis* from its burrow in the sand at the bank of the river. The ant had the pupa about the head and carried it off despite its struggles. Both the Gonomyia and the formicid were common and the tragedy as described was not accidental.

The Pemphredonidae (Mimesinae) and the Crabronidae, fossorial wasps in the Hawaiian Islands, bear an important relationship to the smaller Tipulidae dwelling in the same haunts. Writing of the Mimesinae, a subfamily of the Pemphredonidae, Perkins (1913:lxxxv) says:

> All the Hawaiian species of both genera are true forest insects and most of them may be seen in large numbers, where they occur, flying around ferns and bushes in sunny places. The males are often much more numerous apparently than the females, but this is due to the more retiring habits of the latter, which, when they have begun to provision their nests, frequent dark, shady and damp places in search of their prey. This consists of the endemic Limnobiidae or daddy longlegs, which live in such places. . . . Although I have often watched females of these wasps returning with prey to their burrows, it was always Tipulidae that they carried to the nest. Their burrows are usually made in the ground and are often drilled down from beneath a stone, this no doubt serving to keep the burrow sufficiently dry.

Referring to Limnobiinae, Perkins says (page clxxxii of the same reference):

The species of Dicranomyia are endemic, and to the five described, others and perhaps many more will, no doubt, be added. They are common insects, sometimes attracted by light and sometimes observed at rest in the daytime, or on the wing in the dark cavity of some hollow tree. In the latter case a number are usually seen flying together, rising and falling in their flight in the narrow space of a few feet. We have bred one or more species from decayed wood, overgrown with damp moss. These fragile flies are the favourite prey of the endemic predaceous wasps of the family Mimesidae, and some of the Crabronidae likewise gather them. Consequently one may find the females of these wasps investigating damp, dark places, where the Dicranomyia are likely to be found, but which ordinarily would have but little attraction for such sun-loving insects.

Writing of the Crabronidae, Perkins says (page lxxxvi of the reference cited):

Xenocrabro hawaiiensis on one occasion was caught carrying off Lispe [Anthomyiidae] and on another occasion a species of the limnobiid Dicranomyia.

De Meijere (1920:59) records *Crabro* (*Rhopalum*) *tibiale* as provisioning its nest principally with *Molophilus armatus* Meij.

Parasitic natural enemies

External parasites

Besides the predatory forms just considered, the various stages of the existence of many crane-flies are threatened with parasites which are equally effective altho more insidious in their method of attack. There are unquestionably many parasites of crane-flies concerning which nothing at all is known at this time. It is inconceivable that such species as *Holorusia grandis*, *Tipula abdominalis*, and other large and common forms do not serve as hosts for parasites as yet unknown. It is this field of investigation that now promises some of the most valuable results.

Hexapoda.— The only parasitic insects of which the writer knows are the dipterous Tachinidae. Glover (1874) states that in Europe certain Tipulae are destroyed by a proctotrupid parasite of the genus Diapria Latreille. Kieffer, in his monograph of the Diapriidae (1911), does not mention this and the writer has not seen it referred to elsewhere. It is probable that the reference pertains to some of the smaller Tipula-like forms of another family. However, it is very strange that one or more of the many families of parasitic Hymenoptera do not infest some stage of the Tipulidae, and it may be confidently predicted that such parasites will one day be discovered.

Tachinidae: Most of the species of the interesting genus Siphona (Bucentes) are parasitic on the caterpillars of various Lepidoptera. Two have been recorded as parasites of the larvae of species of Tipula. The better-known of these is *Siphona cristata* (Fabr.), a constant parasite of the larvae of *Tipula maxima* (Beling 1886, Czizek 1913, Riedel 1913, Thompson 1915). The method of attack by the parasite has been described by Roubaud (1906). The large, massive larvae of this species of crane-fly are amphibious or semi-aquatic, living near the margins of streams and other bodies of water. They live in the mud or in the water beneath the surface, at times coming up to breathe the air thru the two large spiracles at the posterior end of the body. It is at this time, when the spiracular disk is projected thru the surface film and the spiracles are open, that the tachinid is supposed to dart down and deposit its eggs in the open stigmata. The young parasite is somewhat elongated, yellowish orange in color, and about a millimeter in length, and is completely inclosed in a firm, membranous cyst. It is connected with one of the two principal tracheal trunks of the host by a sort of chitinized calyx which opens into the trachea. At the time of their pupation the parasites detach their organs of fixation, and with their heads perforate the skin of the host and enter the humic earth. In nature this departure coincides almost exactly with the time of leaving the water by the host for the purpose of pupation in the earth. The pupal duration of the parasite is about three weeks. Rennie (1912) gives *Siphona geniculata* (De Geer) as a parasite of an undetermined species of Tipula.

Species of the genus Admontia are important parasites of the larvae of crane-flies. In Europe, *Admontia amica* (Meig.) is parasitic on species of Tipula, while in America *A. pergandei* Coq. is an important parasite of the smoky crane-fly, *Tipula cunctans* (Hyslop, 1910:128). In the collection of the Illinois Natural History Survey are several specimens of *A. pergandei* bred from larvae of the smoky crane-fly (larvae taken at Urbana, Illinois, parasites emerged October 9 to 25, 1900). Averin (1913) and Lutchnik (1916), in Russia, record the larvae of a Tipula, in one case at least — that of the economic species *T. oleracea* — as being very heavily infested by an undetermined tachinid which may have been the Admontia species mentioned above.

A third genus of Tachinidae, Sturmia, has recently been reported to the writer by J. D. Tothill as being parasitic on the larva of a large crane-

fly, undoubtedly a tipuline form. The larva was found at Chelsea, near Ottawa, on May 27, 1906, by Dr. James Fletcher, the parasite issuing on June 27. The tachinid is to be described as *Sturmia tipulensis* Tothill.

The genus Trichoparia is parasitic on Ctenophora and its allies.

Altho the Tachinidae are the only dipterous parasites that are definitely known from the Tipulidae, the writer has a record of a species of Phaonia, of the family Anthomyiidae, which possibly is a parasite. Among some Diptera sent to Malloch for naming was one specimen of a Phaonia bearing the label " Bred from tipulid pupa, acc. no. 14022." The writer is indebted to R. H. VanZwaluwenburg for the following facts concerning this specimen: The material was taken by Harry L. Parker on June 6, 1916, on South Mountain, near Hagerstown, Maryland. Under litter and growth of Virginia creeper on rock a tipulid pupa was found. The pupa had been eaten out inside and there was a hole in the side of its body. About a half inch away from this pupa was found a newly formed pupa of an anthomyiid fly. The adult emerged on June 23, 1916, and was pinned. It is possible, of course, that the Phaonia was merely feeding on the tipulid, as recorded for this genus elsewhere in this paper (page 728), and that the species is a predatory enemy rather than a parasite.

Arachnida.— Young mites of species of Trombidium, Rhyncholophus, and other genera of Arachnida, are frequently found attached to the body and the wings of adult crane-flies. This attachment is by anal filaments, and it is doubtful whether any real injury results to the host therefrom. These cases are probably instances of phoresy to provide a means of dispersal of the mite. At various times the writer has found in northeastern America a large number of adult crane-flies so infested, and practically every genus and many species are included among the number.

Fungi.— Among the enemies of crane-flies, both to the immature and to the adult stages, probably none are more lethal in their action than certain parasitic fungi. The largest groups of insect-fungous parasites are the Entomophthoraceae (Phycomycetes) and the Laboulbeniaceae (Ascomycetes). Dr. Roland Thaxter informs the writer that, altho the latter group infest other Diptera, he has never seen specimens on Tipulidae, and none have been recorded in the literature. The writer is greatly indebted to Dr. Thaxter and to A. T. Speare, Government Mycoentomologist, for data on this subject. Dr. Thaxter sent to the writer for determination a considerable number of specimens of crane-flies with their para-

sites, these including the types of many of his Entomophthoraceae and some new species not yet described. From these data and the literature the following notes may be given:

Class, Phycomycetes
Family, Entomophthoraceae

1. *Entomophthora (Empusa) pachyrrhinae* Arthur. On the larvae of *Nephrotoma ferruginea*; a manuscript name.
2. E. (E.) *sepulchralis* (Thaxt.). On an adult Tipula of the *subunicolores* group.
3. *E. (E.) caroliniana* (Thaxt.) [= *E. arrenoctona* Giard]. On an adult male of *Tipula entomophthorae.*
4. *E. (E.) arrenoctona* Giard. On male adults of *Tipula paludosa* (Giard 1888, Villeneuve 1910, Picard 1913).
5. *E. (E.) tipulae* Fres. On *Tipula maxima* (Lohde, 1872).
6. *E. (E.) conglomerata* (Sorokin). A species which is probably this one is recorded by Thaxter on larvae and adults of Tipulidae.
7. *E. (E.) sphaerosperma* Fres. Recorded by Thaxter from adult Tipulidae.
8. *E. (E.) grylli* Fres. Recorded on at least two occasions from the adult flies of *Tipula ultima* Alex. [= *T. flavicans* Fabr.].
9. *E. (E.) punctata* Thaxt., ms. On adult females of *Pseudolimnophila noveboracensis.*
10. *E. (E.) dipterigena* (Thaxt.). On the adult flies of several genera of Limnobiinae, as follows: *Molophilus hirtipennis*, *Limnophila aprilina*, *Pseudolimnophila nigripleura*, *Ulomorpha pilosella*, *Penthoptera albitarsis.*
11. *Isaria* sp. On adults of *Dicranomyia pubipennis.* Additional undetermined species of this same genus on various tropical Tipulidae.

Class, Hyphomycetes.
Family, Mucediniaceae.

12. *Sporotrichum densum* Link. On *Tipula cunctans* Say [= *T. infuscata* Lw.] (Hyslop, 1910:130).

Internal parasites

Crane-fly larvae and adults are infested by numerous protozoan and bacterial parasites, the more conspicuous and constant being the Sporozoa (Gregarinidae) and the Bacteria. General references to this subject may be found in Léger (1892), Labbé (1899), and Minchin (1903). More especial references are made to the parasites of Ptychoptera by Léger and Duboscq (1909), to those of Dicranota by Miall (1893: 237), to those of Ctenophora by Anthon (1908:542), and to those of Tipula by Mackinnon (1913). In the case of Ctenophora the parasites were frequent between the cells of the alimentary canal, especially in the proventricular caeca. The writer has found a large gregarine very abundant in the alimentary canal of the larva of *Pedicia albivitta*, many of the individuals being very heavily infested. Gamkrelidze (1913 b) records gregarine and nematode parasites in Gnophomyia larvae.

The more important recorded protozoan parasites are as follows:

Class, Sporozoa.
Subclass, Telosporidia.
Order, Coccidiomorpha.
Family, Adeleidae.

1. *Adelea tipulae* Léger. In the intestine of species of Tipula.

Order, Gregarinida.
Family, Gregarinidae.

2. *Hirmocystis polymorpha* (Léger, 1892:113). In the intestine of the larva of *Limnobia* sp.
3. *H. ventricosa* (Léger, 1892 :111). In the alimentary canal of *Tipula oleracea*, *Nephrotoma pratensis*, and other species.
4. *Gregarina longa* (Léger, 1892:117). In the alimentary canal of a species of Tipula.

Family, Actinocephalidae.

5. *Actinocephalus tipulae* Léger (1892:141). In the alimentary canal of Tipula larvae. Probably the same species has been recorded from the larvae of a species of Ctenophora.
6. *Pileocephalus striatus* Léger & Duboscq (1909:887–893). In the mid-intestinal epithelium of the larva of *Ptychoptera contaminata*. The Pileocephalus live in the epithelium of the mid-intestine, attaching themselves to the epithelial cells and hypertrophying the adjoining tissues. They obtain their nutriment from the food that penetrates into the cells.

Family, Stylorhynchidae.

7. Near Stylorhynchus (Miall, 1893:237). In the stomach of larvae of *Dicranota bimaculata*.

Subclass, Neosporidia.
Order, Cnidosporidia.
Suborder, Microsporidia.
Family, Nosematidae.

8. *Nosema strictum* Monz. (Moniez, 1887). In muscles, conjunctive tissue, and other parts of *Nephrotoma pratensis*.
9. *Gurleya francottei* Léger & Duboscq (1909:894). In the epithelium of the mid-intestine of the larva of *Ptychoptera contaminata*.

Class, Flagellata.
Family, Trypanosomidae (Herpetomonadidae).

10. *Crithidia campanulata* Léger. At the juncture of the mid- and hind-intestines in the larva of *Ptychoptera contaminata* (Léger & Duboscq, 1909:898–900).

The writer is indebted to Dr. R. Kudo for assistance in determining the terminology used above.

Bacteria are frequently found in crane-fly larvae. Léger and Duboscq (1909:900–901) record undetermined spirochaetes in the epithelial cells of the posterior part of the mid-intestine of *Ptychoptera contaminata*. Dr. Hugh Glasgow, of the Geneva Experiment Station, informs the writer that in Illinois a large tipulid larva, probably that of *Tipula abdominalis*, living in the leaf-drift of prairie streams, is heavily infested with bacteria. Most of the specimens observed had an abundance of small coccus and spirochaete forms, with occasional specimens of a gigantic bacillus measuring from forty to eighty microns in length and disporous. These large bacilli infest the hind-gut of the larva.

HISTORICAL SUMMARY OF THE IMMATURE STAGES

The discovery and description of the immature stages of crane-flies has by no means kept pace with the taxonomic work that has been done on the adult flies. There are a very large number of common species in every country concerning whose early stages nothing at all is known, and the knowledge that exists concerning a comparatively small number results from the labors of a few students. Among these may be mentioned Beling, Mik, Brauer, Hart, Needham, and Malloch. Some other workers have given excellent descriptions of single species, while still others have contributed important treatises on the anatomy, morphology, histology, and related subjects of the different species. The descriptions of the earlier workers are, for the most part, of historical interest only, but in a few cases they are exceptional and are still the main source of information concerning certain species. Many of the foremost workers on the taxonomy of the adult flies have summarized the earlier writings on the immature stages but have themselves contributed little to the subject, among these being Schiner, Loew, Osten Sacken, Skuse, and Brunetti. The following chronological summary gives an indication of the more important work that has been done on this phase of the subject:

1722	Frisch	*Tipula oleracea*
1740	De Réaumur	Ptychoptera, Tipula
1776	De Geer	Phalacrocera, Ctenophora, Tipula
1803	Schellenberg	Cylindrotoma
1829	Stannius	*Limnobia xanthoptera* [=*bifasciata*]
1832 (Posthumous)	Lyonet	Ptychoptera
1833	Bouché	*Dictenidia* sp., *Tipula* sp.
1834	Von Röser	*Hexatoma nigra*
1838	Boie	Cylindrotoma
1840	Dufour	Trichocera
1842	Zeller	Cylindrotoma
1846	Bremi-Wolf	Trichocera, *Limnobia xanthoptera* [=*bifasciata*], Nephrotoma
1849	Perris	Trichocera, *Limnophila dispar*, Ula, Tanyptera
1854	Brauer, Egger, and Frauenfeld	Chionea
1867	Nowicki	*Dactylolabis wodzickii*
1872	Weyenbergh	Ctenophora, Dictenidia: anatomy and histology
1873–86	Beling	The immature stages of 69 species of European Tipulidae, including 30 species of Tipula
1875–76	Hammond	*Tipula oleracea*: anatomy
1876	Grobben	Ptychoptera: anatomy
1876–1902	De Rossi	*Liogma glabrata*, *Tanyptera atrata*
1880	Hermann	*Tanyptera atrata*
1882–1900	Mik	Discobola, Elliptera, Dactylolabis, *Tipula rufina*, etc.

1883	Brauer	Important work on the classification of the immature stages
1884	Gercke	*Rhamphidia longirostris, Tanyptera atrata*
1890	Van Gehuchten	Ptychoptera: histology of alimentary canal
1893–97	Miall	Dicranota, Phalacrocera
1895 [1898]	Hart	Pioneer American worker; Bittacomorpha, etc.
1897	Bengtsson	Phalacrocera: anatomy
1900–09	Johnson	Teucholabis, Aeshnasoma, etc.
1901	Kellogg	*Holorusia grandis* (as *rubiginosa*): anatomy
1901	Müggenberg	*Liogma glabrata*
1901–08	Needham	*Dicranomyia simulans, Pedicia albivitta*, Rhaphidolabis, *Tipula ultima* (as *flavicans*)
1907–08	Steinmann	*Triogma trisulcata*
1908	Holmgren	Phalacrocera: mouth parts
1908	Anthon	*Ctenophora angustipennis*: anatomy
1908–09	Pastejrík	*Limnobia xanthoptera*, Ctenophora
1908–09	Müller	*Triogma trisulcata*
1909	Brocher	*Tipula lunata*
1909	Greene	*Tipula trivittata*
1909	Thienemann	*Dicranomyia trinotata*
1910	Brown	*Tipula maxima*: anatomy
1910	Hyslop	*Tipula cunctans* (as *infuscata*)
1911	Vimmer	Ctenophora, *Tipula oleracea*: mouth parts
1911–16	De Meijere	*Trentepohlia pennipes, Tipulodina pedata*, and several European species
1912	Keilin	Trichocera: morphology
1913	Caudell	*Tipula ultima* (as *flavicans*)
1913	Gerbig	Anatomy of the respiratory system of many European species of Tipulidae
1913	Picado	*Trentepohlia bromeliadicola*
1914	Del Guercio	*Tipula oleracea*
1914–16	Topsent	*Ptychoptera albimana*
1914–19	Alexander	Dicranoptycha, Ula, Eriocera, Hexatoma, Penthoptera, Liogma, Prionocera, *Tipula arctica*
1915	Swezey	*Dicranomyia foliocuniculator*
1915	Lovett	*Ctenophora angustipennis*
1915	Wesenberg-Lund	Dicranota, Phalacrocera, Triogma
1915–17	Malloch	*Limnobia immatura*, Gnophomyia, and, in his uncertain material, Antocha, Elephantomyia
1916–17	Rennie	*Tipula paludosa*
1918	Cameron	*Cylindrotoma splendens*
1920	Hudson	*Gnophomyia rufa; Limnophila sinistra*
1920	Lenz	Thaumastoptera, Cylindrotominae

ECONOMIC IMPORTANCE

The larvae of some species of crane-flies, almost all belonging to the genera Tipula and Nephrotoma, often do considerable damage to various crop species, the injury being largely caused by the larvae devouring the roots and thus killing the plants. Certain of these crane-fly species, as *Tipula oleracea, T. paludosa*, and *Nephrotoma maculata* in Europe, and *Tipula bicornis* and *Nephrotoma ferruginea* in America, have long been known, but several others have come into prominence only within the

past ten years, notably *Tipula parva* Lw. (supposition) in Japan, and *T. cunctans* and *T. simplex* in North America. The more important outbreaks of this nature which have been recorded are as follows.

Species affecting herbaceous plants

Nephrotoma ferruginea has been reported by Webster (1891, and 1893 a: 243–245) as injuring young wheat in Indiana, the injury in some cases being estimated at fifty per cent.

Tipula oleracea is the best-known European species in this group, infesting a wide range of plants. The more important outbreaks of this species as recorded are as follows: Ewert (1899) reports from Germany an unusually severe attack, in which the larvae of this species and of *Tipula nigra* did a considerable amount of damage to the roots of grasses. They were so abundant that from ten to twenty could be found in the area of one square foot. Grasses in the infested area were completely destroyed. Ormerod (1885, 1886, 1900) records serious injury by *T. oleracea* to pastures and meadows in England, and recommends applications of guano either alone or mixed with salt, kainit, or superphosphate. This species has been recorded also as being a serious pest in Ireland (Anonymous reference, 1904 b) in grainfields and meadows, and careful plowing and the use of fertilizers for its control are advised. Schoyen (1903), in Norway, reports serious injury to meadows and pastures, as well as to cereals and young cabbage plants. Del Guercio (1914) records serious injury in the Italian rice fields.

A few additional outbreaks of *Tipula oleracea* may be mentioned. Barthou (1913) records injury to canes (raspberry, strawberry, and others) in France. Désoil (1914) reports injury to meadows in France, and Ritzema Bos (1915) to meadows in Holland.

Tipula paludosa is reported by Lind, Rostrup, and Kolpin Ravn (1914 and 1915) as causing serious injury to oats and barley in Denmark, and Rennie (1916 and 1917) reports the same species as injuring corn and pastures in England.

Tipula flavolineata is reported by Sopotzko (1916) as injuring clover in Russia. The specific identity, however, is probably erroneous, as this species lives almost entirely in decaying wood (Beling, 1873 b: 581–582).

Onuki (1905) records *Tipula parva* Lw. (supposition) as one of the serious rice pests in Japan. In some localities from sixty to ninety per

cent of the seedlings have been destroyed by this species. The larvae apparently cannot exist in water for any long period of time, and so may be killed by flooding the fields for from six to thirty-six hours. Del Guercio (1914) offers the same recommendation for the control of *T. oleracea* in the Italian rice fields.

Tipula bicornis has been found in grass and clover lands in Illinois by Forbes (1890), and on clover in Indiana by Webster (1892 a).

Tipula cunctans, as recorded by Hyslop (1910: 126, as *T. infuscata*), works largely on Japan clover and other leguminous plants. The larvae are often exceedingly numerous, as many as two hundred having been found in an area covering but little more than one square foot of soil. They destroy the plants by devouring the roots and sucking the juices. It is recommended that the infested fields be plowed under before the adult flies emerge (in the autumn), and the following season be planted to corn or potatoes or else left fallow.

Tipula simplex has been found on pasture land and alfalfa in California by Doane (1908) and by Carnes and Newcomer (1912). Doane (cited by Hyslop, 1910: 120–121) also reports an outbreak of this species on wheat and grass lands and in clover fields in central California in 1907, and states that thousands of acres of these crops were stripped of their verdure.

The following summary gives the various species of plants that are damaged or destroyed by crane-flies in general. Very many of the injuries reported for *Tipula oleracea*, however, are omitted.

Family	Crop	Species	Authority
Gramineae	Wheat	*Nephrotoma ferruginea*	Webster (Indiana), 1891, 1893 a
	Wheat	*Tipula simplex*	Hyslop (California), 1910
	Wheat	Tipulidae	Stedman (Missouri), 1902
	Corn	*Tipula paludosa*	Rennie (England), 1917
	Corn	*Tipula* sp.	Kirk (New Zealand), 1895
	Barley	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1915
	Barley	*Tipula* sp.	Wahl and Müller (Germany), 1914
	Barley	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
	Oats	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1914, 1915
	Rice	*Tipula oleracea*	Del Guercio (Italy), 1914
	Rice	*Tipula parva*	Onuki (Japan), 1905
	Cereals	*Tipula oleracea*	Anonymous reference (Ireland), 1904 b
	Cereals	*Nephrotoma pratensis*	Hollrung (Germany), 1898

Family	Crop	Species	Authority
Gramineae	Meadows and pastures	*Tipula bicornis*	Forbes (Illinois), 1890
	Meadows and pastures	*Tipula simplex*	Carnes and Newcomer (California), 1912
	Meadows and pastures	*Tipula oleracea*	Anonymous reference (Ireland), 1904 b
	Meadows and pastures	*Tipula oleracea*	Désoil (France), 1914
	Meadows and pastures	*Tipula paludosa*	Rennie (England), 1917
	Meadows and pastures	*Tipula* sp.	MacDougall (Scotland), 1915
	Meadows and pastures	*Tipula* sp.	Ritzema Bos (Holland), 1915
	Meadows and pastures	*Tipula* sp.	Marchal and Prillieux (France), 1916
	Meadows and pastures	*Tipula oleracea*	Ormerod (England), 1885, 1886, 1900
Liliaceae	Tulips (bulbs)	*Nephrotoma maculata*	Collinge (England), 1911
	Onions and garlic	*Tipula oleracea*	Vassiliev (Russia), 1915
Cruciferae	Cabbage	*Tipula oleracea*	Schoyen (Norway), 1903
	Cabbage	*Tipula oleracea*	Averin (Russia), 1913
	Cabbage	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
	Cabbage	*Tipula* sp	Lutchnik (Russia), 1916
	Cabbage	*Nephrotoma* sp	Lutchnik (Russia), 1916
Polygonaceae	Buckwheat	*Tipula oleracea*	Goriatchkovsky (Russia), 1915
Rosaceae	Roses	*Nephrotoma lineata*	Schaufuss (Germany), 1901
	Raspberry and strawberry	*Tipula oleracea*	Barthou (France), 1913
Leguminosae	Clover	*Tipula bicornis*	Webster (Indiana), 1892a
	Clover	*Tipula bicornis*	Forbes (Illinois), 1890
	Clover	*Tipula flavolineata*	Sopotzko (Russia), 1916
	Clover	*Tipula oleracea*	Del Guercio (Italy), 1914
	Japan clover	*Tipula cunctans*	Hyslop (Tennessee), 1910
	Alfalfa	*Tipula simplex*	Carnes and Newcomer (California), 1912
	Peas	*Tipula paludosa*	Lind, Rostrup, and Kolpin Ravn (Denmark), 1914
Umbelliferae	Carrots	Tipulidae	Lesne (France), 1905
Solanaceae	Potatoes	*Tipula oleracea*	Beling (Germany), 1887
	Potatoes	*Tipula lateralis*	Cameron (Scotland), 1917
	Potatoes, stored	Trichocera	Johannsen (Maine), 1910
	Potatoes, stored	Trichocera	Carpenter (Ireland), 1912
Compositae	Cardoon	*Tipula* sp	Lesne (France), 1908

Species affecting woody plants

Species that injure or destroy living trees or shrubs are not common, and the damage that they do is almost entirely of a minor nature.

Ctenophora angustipennis is recorded as doing secondary damage to prune trees in Oregon (Lovett, 1915). Fuchs (1900) records four species — *Tipula scripta, T. marginata, Nephrotoma cornicina* [as *iridicolor*], and *N. quadrifaria* — as injuring young plants of both deciduous and coniferous species. Taschenberg (1880:54) describes *Tipula flavolineata* and *Nephrotoma crocata* as destroying year-old seedlings of fir and larch. Matsumura (1916:466) records the larva of *Nephrotoma makiella* as injurious to the mulberry (Morus) in Formosa.

METHODS OF EXPERIMENTAL PROCEDURE

Collecting

The larvae of the larger species of crane-flies, such as those of the genera Tipula, Pedicia, and Eriocera, may be readily discovered in the field, but the immature stages of the smaller Tipulidae are not so easily found. It is necessary to bring into the laboratory large quantities of the material in which the immature stages are supposed to be living, and there to examine it with considerable care. In the case of mud or earth, it is better to wash away the finer silt particles and examine the residue. The writer has found it most convenient to use a Simplex water-net, placing in it a handful of earth and holding it underneath a running faucet. The mesh of this net is of sufficient diameter to retain any crane-fly larvae except the very young stages. When the fine particles have been removed the residue can be examined in water in white enameled or porcelain dishes, and the larvae and pupae may be easily detected in the water. Numerous associated forms of life will be found, and these should be preserved or recorded.

The immature stages of wood-inhabiting species are most easily found in the field by a patient and painstaking examination of the removed bark and the exposed parts of the tree stump or trunk. Moss-inhabiting species, such as those of Liogma and many tipuline forms, may be shaken from their haunts onto a piece of white oilcloth, where they are easily observed.

Killing and preserving

The larvae and pupae to be studied should be dropped into boiling water for a brief instant. The larva, on contact with the water, at once expands to its maximum size, the spiracular disk is spread wide open, and the anal

gills are completely everted. The specimens should be placed in 4-per-cent formalin or, preferably, 70- to 75-per-cent alcohol. Large, fleshy larvae, such as those of the Tipulinae, should be slit at the third or the fourth abdominal segment to allow easy penetration of the preservative. Other notes on preserving material are given by Banks (1909) and by Williamson (1916).

Study

In the study of the gross material, both the binocular and the compound microscope may be used. A special word on the preparation of the head capsule of the larva may be helpful. In removing the head capsule from the body it is generally easiest to slit longitudinally the thoracic segments back of the head and pull the capsule thru this incision. In forms with compact and massive capsules, the thorax and the head may be snipped off and the head everted after the manner of turning the finger of a glove. The capsule should be left in a 5-per-cent solution of caustic potash until all the fleshy parts have been removed. It should be dissected out so that all the mouth parts are isolated and rendered distinct for study. Then follow the usual processes of washing and dehydration, and the final mounting in canada balsam.

Various means are available for examining the spiracular disk. The specimen may be placed in a watch crystal under water and held firmly in place by a piece of glass, as, for example, a broken microscope slide. By holding a heavy piece of glass over the anterior end of the body, the posterior end may be bent at a right angle and bolstered in place by two or three other glass fragments so that the disk is directed straight upward and its details are easily examined. Other methods, such as embedding the anterior end of the larva in paraffin in a deep dish and submerging the body, may be followed. It must be emphasized that in alcoholic gross material the study should be conducted under alcohol or water.

The measurements of the pupa — abbreviated in the text as *d.-s.* (dextro-sinistral) for the width and *d.-v.* (dorso-ventral) for the depth — are taken opposite the wing pad.

Rearing

In order to rear the immature stages of crane-flies successfully the natural haunts should be imitated as closely as possible. In the case of wood-inhabiting species, large pieces of the material in which the larvae

are working may be brought into the laboratory and placed in the breeding cages. This method may be followed with species of Tanyptera, Ctenophora, and other genera.

Fungicolous species, as a rule, also are easily reared. The entire fungus in which the specimen is found should be brought into the laboratory and placed in a jar on a bed of clean sand. The sand takes up the liquids produced by the disintegration of the fungus and provides a place for pupation. Species of Limnobia, Ula, and other forms are reared in this manner.

The chances for error in rearing are many. One must be certain that there are no other larvae in the breeding jar with the one that is being reared; else one of these other larvae might transform and emerge first, and the results would be altogether misleading. The writer has had this happen in his breeding cages, even after the utmost care had been used to guard against it. Beling, the great German student of the immature stages of crane-flies, made a few mistakes in the same way; as, for example, in the case of his Trimicra, the larvae that he describes being pediciine and probably a species of Dicranota or the young larvae of a Tricyphona. What happened, presumably, was that Beling found these pediciine larvae and placed them in rearing; in the same cage, but unknown to the breeder, was a larva of Trimicra which emerged, and naturally Beling thought it came from one of the larvae that he had placed in rearing. It is usually easy to check up such errors. Thus, the writer has placed in rearing the larvae of Penthoptera and, to his surprise, had adults of *Limnophila adusta* emerge. Obviously larvae of *L. adusta* got into the cage in spite of precautions, and emerged first. When closely related species are concerned, however, it becomes a hard matter to straighten the tangle. Hence a species cannot be reared too many times, since each rearing checks up the previous results.

The precaution to be taken in the case of mud-inhabiting or sand-inhabiting species is to see that the mud or sand is baked or thoroly desiccated in order to destroy all life in it. Then it may be remoistened, and the larva or larvae chosen to rear may be put into the earth without the chance that some unknown larva may be lurking in the medium and may emerge first, and so bring about confusion.

The writer has found that the most satisfactory way to rear small tipulid larvae found in earth or sand is to place a small amount of baked

earth from their haunts in a 4- or 6-dram shell vial, moisten the earth, and place a thin layer of moss over it. The vial should not be corked, but should be covered with a piece of cheesecloth held in place by rubber bands. In the case of carnivorous species, as the Hexatomini and the Pediciini, individuals should be isolated in vials, but the herbivorous species may be bred in large numbers in single containers. The predatory forms are usually distinguished without difficulty by their extremely active, snakelike motions, the other species being more sluggish in their actions.

Strictly aquatic forms, such as Antocha, are reared only with great difficulty. These species can survive only in rapidly flowing, well-aërated water, and it is usually a difficult matter to imitate this condition successfully. The best plan is to place rearing cages in the natural haunts of the larvae. This can be done if a suitable location is sufficiently close at hand and free from disturbance by inquisitive passers-by. The chief source of danger to breeding cages in natural streams is that a sudden rise of water may suffocate the larvae or wash the cages downstream, or else may destroy the contents of the cage by a thick deposition of silt. Lotic species that are discovered in streams far removed from the laboratory can be transported alive for long distances in folds of wet cheesecloth. The writer has found this to be the most satisfactory way to keep advanced pupae alive until they are ready to emerge as adults.

In general, the writer has found species of the tribe Pediciini the most difficult to rear, and the Limnobiini and the Eriopterini perhaps the easiest. Mud-inhabiting species are easily reared, but species from rushing torrents are at the opposite extreme and it is almost an impossibility to bring some of these species thru to the adult condition.

TYPES OF THE IMMATURE STAGES

The material on which this study is based was almost entirely reared. It seems desirable that these authentic specimens of the larva and the pupa should be so designated that they will have a value greater than that possessed by ordinary specimens. No terms for the designation of types of the immature stages are known to the writer, and the two that are needed in this paper are here defined as follows:

Nepionotype, The type of the larva.
Neanotype, The type of the pupa.

The type specimen should, of course, be selected only when there is absolute certainty of the identification, and in most cases this determination can be made only by rearing the species. After the species has been reared (this should be done many times, if possible, in order to check up the identity), a good representative specimen may be chosen as the type of the stage. In the cases in which the species is known only from a single specimen, the nepionotype may be the larval skin, the neanotype the pupal skin. The remaining specimens of the original series become paratypes. The types of the immature stages possess fully the value of the type of the adult and should be as carefully preserved. The types herein designated are in the collection of the writer. They are preserved in alcohol, but the larval heads of most species have been removed, treated with caustic potash, and mounted in balsam.

EXTERNAL MORPHOLOGY

The larvae and the pupae of crane-flies show considerable diversity in their general form. The fundamental plan of structure remains much the same thruout the group, but the details are widely different and furnish the characters in use for the separation of the various tribes and lesser divisions.

The immature stages of crane-flies have evolved more rapidly than have the adult flies, and in many features they show a greater specialization. The head capsule of the larva seems to be the most constant feature, the same fundamental type of structure recurring in the generalized members of all the various groups, indicating a close phylogenetic relationship. On the other hand, the respiratory organs of both the larvae and the pupae vary greatly in the different species and are obviously molded by habitat. The often-repeated statement that the inside of an organism shows what it is, while the outside shows where it has been, is well illustrated here.

The larva

General features

The form of the larval body is, as a rule, moderately elongated and usually terete. The head is eucephalous and non-retractile in the three families Tanyderidae, Ptychopteridae, and Rhyphidae. It is incomplete and more or less retractile in all the species of Tipulidae. The body is shortest in the more generalized forms, becoming greatly elongated

in many Eriopterini and some Limnobiini (Dicranoptycha). It is made up of the composite head capsule, three thoracic segments, and nine evident abdominal segments. In some species all the abdominal segments are subdivided, respectively, into a narrow basal and a usually broader posterior ring, or annulus; in other species only the basal segments are so subdivided. The integument is usually covered with a dense appressed pubescence and often bears setae, or pencils of hairs, or, in some Cylindrotominae, spinous projections.

Respiration is characteristically metapneustic; in the Rhyphidae it is amphipneustic, in Antocha apneustic. The typical metapneustic forms often show vestigial lateral spiracles, but these are not functional in any species known to the writer and the peripneustic type of larva is still unknown in this group of Diptera. The spiracles are placed at the ends of the long breathing tubes in the Tanyderidae and the Ptychopteridae. In the Tanyderidae, the Tipulidae, and the Rhyphidae the disk is surrounded by a varying number of lobes which are rarely indistinct, these ranging in number from two to eight. Anal gills are found in representatives of almost all the major groups of crane-flies, and their loss is a result of habitat and non-usage. In wood-inhabiting species the gills are often modified into blunt lobes, having the evident function of propulsion by shoving.

Body form

As already stated, in the majority of crane-fly larvae the body is terete or approximately so, but in some species it is decidedly depressed with the ventral surface flattened. Such forms are Dactylolabis, some Cylindrotominae, and some Tipulinae. The integument is produced into elongate spines and blades in almost all species of Cylindrotominae, similar conditions being suggested in a few tipulines. A definite arrangement of setae (chaetotaxy) obtains. The basal abdominal ring is provided with a transverse creeping-welt in the Limnobiini and in some Hexatomini and Pediciini, as well as in a few other forms. In some genera, as Epiphragma, this welt is practically naked; in others it is covered with a microscopic scurfiness; while in still others (Dicranota) it is separated into distinct paired prolegs, which are armed with circlets of chitinized hooks that lessen in size from the tips basally. The welts are both dorsal and ventral in position in many Limnobiini and in some Pediciini (Rhaphi-

dolabina), or are ventral only (Rhamphidaria, Ularia, Epiphragmaria, and most Pediciini). In number they range from four (on abdominal segments 4 to 7) in most Pediciini, to five or six (on abdominal segments 2 to 7) in Ularia, Epiphragmaria, and other forms.

Organs of respiration

The spiracular disk.— The posterior end of the body is usually truncated, bearing the two spiracles and surrounded by a number of fleshy lobes. These lobes vary much in their shape and armature, and range in number from two in the Pedicaria and the Antocharia to six or eight in the Tipulinae. The inner faces of the lobes are often lined with brown or black horny plates, which serve as points of attachment for the longitudinal muscles. Their arrangement and distribution are of great service in specific classification.

The Limnobaria usually have the lobes surrounding the spiracular disk indistinct; the Antocharia have two long ventral lobes; the Rhamphidaria five lobes; the Ellipteraria and the Dicranoptycharia four lobes.

In the Eriopterini, the Elephantomyaria and some Eriopteraria have four lobes; the majority of species of the latter division have five. In these last-named species the disk is almost squarely truncated, and the five lobes are subequal and stellate in appearance.

The Hexatomini usually have four lobes, with the ventral pair longer than the lateral pair. In a few cases only (Ularia, Dicranophragma, Poecilostola), a reduced mid-dorsal lobe is present. In the more specialized forms the lateral lobes also tend to reduce, simultaneously with the elongation of the ventral lobes. In this tribe the disk is fringed with long hairs, which are sometimes excessively elongate, especially on the ventral lobes where they appear as long fringes of delicate hairs that spread out on the surface film of the water as broad fans. Such fringes are found in a large number of Hexatomini and also in the Adelphomyaria (supposition). Near the tips of the ventral lobes, but inside this fringe of hairs, are often inserted one or more stiff sensory bristles.

In the Pediciini, the Pedicaria have two lobes and the Adelphomyaria (supposition) have four. In the former division the lobes are ventral in position and are almost naked.

The Cylindrotominae have six rather indistinct lobes in Cylindrotoma, and four in the other genera.

The Tipulinae show six lobes in practically all genera, the only exceptions being that there are eight in a few rare cases of Tipula and five in Dolichopeza, and that lobes are indistinct or lacking in Tanyptera.

In the Rhyphidae (Trichocerinae) the spiracular disk is very similar to that in many Tipulidae, and is surrounded by four lobes. In the Ptychopteridae the very reduced disk is borne at the tip of a slender, retractile breathing tube. In the Tanyderidae the condition is somewhat similar, but here the disk is larger and is surrounded by five lobes at the tip of a long, stout, non-retractile breathing tube.

The spiracles vary greatly in size from very large to small and vestigial, or they may even be lacking in some species of Antocha. They consist of an apparently uniform middle piece surrounded by a radially folded margin, or ring, of various widths, called the *stigmal ring*. Many authors (De Meijere, Mik, Müggenberg, Brown, Keilin, and others) hold that the middle piece is an imperforate chitinized plate and that respiration takes place thru the stigmal ring. Gerbig (1913), however, shows that the middle piece is split across the disk, the cleft being closed by two overlapping membranes. Directly behind the spiracles the tracheae enlarge into the felt chamber, whose walls are provided with long, branched, treelike structures, the branches apparently anastomosing. Surrounding the felt chamber in many larvae are dense masses of air tubes, which make up the tracheal lungs. These tubes are arranged in bundles, which arise in special cavities of the felt chamber; thus, in *Tipula paludosa*, there are about fifty bundles, each of about twenty tubules, making a total of one thousand of these air canals (Gerbig).

The early stages of the larva are quite different from the later developmental stages, as Gerbig (1913:137–140), working on *Tipula paludosa*, has well shown. The prominent six-lobed spiracular disk of the more matured larva is represented in the first developmental stage by four heavily chitinized projections, which bear but few bristles on their outer margin. The dorsal lobes are not evident, but are replaced by eight branched bristles, about equidistant from one another. The spiracles are oval, not circular as in the grown larva, and project a little beyond the level of the disk. The writer has noted several first-stage larvae with an appearance almost as described but showing several points of difference. The immature larvae of Phalacrocera are described elsewhere in this work (page 963).

Anal gills.— In the Ptychopteridae and in the Tanyderidae there is but a single pair of anal tracheal gills. In the former these are very small and are cylindrical, in the latter they are large, branched, fanlike structures. In the Tipulidae the anal gills number from four in most Limnobiinae to six or eight in the Tipulinae. The increase in number is brought about by a division of the original gill of each side. In generalized forms, as Antocha, Pedicia, and others, the anal gills are constricted into segments, the apical ones being more or less telescopic into the preceding ones. As a rule the anal gills are entirely or almost entirely retractile within the body.

In the Tipulinae the gills vary with the genera, being blunt and constructed for propulsion in the wood-inhabiting species, such as those of Ctenophora, Tanyptera, Tipula, and other genera. In the semi-aquatic species of Tipula the number of gills varies from four to eight. In the latter case each of the four principal gills is deeply bifid and the gills are arranged transversely, as in *T. ignobilis*; in species with six gills the posterior branches of the posterior gills are atrophied as a rule; in other species, which have but four gills, the four anterior branches are preserved, the posterior pair being usually atrophied. In Longurio and Aeshnasoma the four anal gills are pinnately branched, each with about six lateral branches. A similar condition is found in the Tanyderidae.

The head

The primitive crane-fly head was undoubtedly of the eucephalous, non-retractile type, as found in the Ptychopteridae, the Rhyphidae, and other families. The retracted head capsule of the Tipulidae is a derived condition.

The massive, compact capsule is found in all of the lower groups of the three subfamilies of the Tipulidae. Such a head is easily derivable from the condition in the Rhyphidae or in the Tanyderidae, for instance. The dorsal median sclerite, the *prefrons*, is almost as large and conspicuous in Ula as in the eucephalous families. The lateral plates that constitute the capsule are shaped like a mussel in the generalized groups, with the posterior incisions shallow. In the more specialized forms, with the capsule greatly dissected, the two plates of either side are entirely separated — the innermost, next to the prefrons, being the *internal-lateral* of De Meijere, and the outermost being his *external-lateral*. The prefrons

is found in all forms with the capsule compact and massive, and is even preserved in many species with the dissected capsule. In many cases, however, it is firmly fused with the internal-lateral plates; or, in some cases, all the plates of the capsule are firmly united and their individual limits are ill-defined. In the generalized forms the clypeus and the labrum are entirely distinct from each other, while in other forms the two lose their individuality by fusion.

The sclerites of the generalized primitive head bear bristles, or setae, of various types and arrangement. In the Tanyderidae the punctures are multisetose; in most Ptychopteridae the setae are branched or somewhat plumose.

The literature on the head capsule and the mouth parts is as follows:

Ptychoptera. De Meijere, 1916: 188–191, figs. 14–20.
Bittacomorpha. Hart, 1898 [1895]: 192, pl. 5.
Trichocera. De Meijere, 1916: 191–194, figs. 21–23.
Limnobia. De Meijere, 1916: 198–201.
Dicranomyia. De Meijere, 1916: 197–198, figs. 32–35.
Dicranoptycha. Alexander, 1919 b: 71, figs. 2, 3.
Elliptera. Mik, 1886 b: 339, pl. 6.
Ula. Alexander, 1915 a: 5–6, pl. 1.
Dactylolabis. Mik, 1894: 261–266, pl. 2; Nowicki, 1867: 341 (as Rhicnoptila).
Limnophila. De Meijere, 1916: 204–206, figs. 49–51.
Eriocera. Alexander and Lloyd, 1914: 21–22, pl. 1.
Hexatoma. Alexander, 1915 c: 146, pl. 1.
Penthoptera. Alexander, 1915 c: 155, pl. 1.
Tricyphona. De Meijere, 1916: 195–196, figs. 29–31.
Pedicia. Needham, 1903: 286, fig. 19.
Dicranota. Miall, 1893: 237–238, pl. 10.
Ormosia. De Meijere, 1916: 201–204, figs. 37–47.
Gnophomyia. Malloch, 1915–17 b: 230–231, pl. 34, fig. 10.
Chionea. Brauer, Egger, and Frauenfeld, 1854: 614, pl. 11.
Phalacrocera. Miall and Shelford, 1897: 344–345; Bengtsson, 1897.
Cylindrotoma. Cameron, 1918.
Liogma. Müggenberg, 1901; Alexander, 1914: 111, pl. 1.
Ctenophora. Anthon, 1908: 544.
Prionocera. Malloch, 1915–17 b: 199, pl. 32, figs. 1–3.
Holorusia. Comstock and Kellogg, 1904: 55, 61–62.
Tipula. Vimmer, 1906, and 1911: 1–6.

In addition to the preceding, the genera Helobia (Beling, Hart, Malloch), Rhaphidolabis (Needham), and Tanyptera have been discussed less fully.

All of the above-named genera are considered in this paper, and the head capsule and mouth parts of the following genera are described also: Protoplasa (supposition), Bittacomorphella, Rhipidia, Rhamphidia, Antocha, Epiphragma, Pseudolimnophila, Pilaria, Ulomorpha, Elephantomyia, Teucholabis, Gonomyia, Erioptera, Molophilus, Adelphomyia

(supposition), Rhaphidolabina, Oropeza, Longurio, Aeshnasoma. The descriptions for the genera are either entirely new or else the characters have heretofore been insufficiently described and figured. The details of structure of the head capsules of nearly fifty genera of crane-flies are now known.

The labrum and the epipharynx.— The labrum is preserved in all crane-fly larvae. It is usually broadly transverse or oval. The dorsal surface is clothed with short hairs, these being longer on the anterior margin, which is often provided also with a limited number of sensory bristles, or papillae. The lateral regions on the ventral, or epipharyngeal, side often bear long tufts of hairs. The epipharynx proper is variously armed in the different groups of crane-flies.

The labium.—The labial region of the capsule is of vast importance in classification, and the location of the constituent parts should be early appreciated. The confusion in terminology of the dipterous larval labium has been partly outlined by De Meijere (1916:253). The principal synonyms are as follows:

Submentum.
Mentum — The pharyngeal plate, or lower lip (Meinert); submentum (Miall); ectolabium (Bengtsson); labial plate.
Prementum — Mentum (Miall); ectolabium (Keilin); endolabium (Holmgren, Vimmer, Bengtsson).
Hypopharynx — Labium (Meinert); mentum (Miall, in Dicranota); endolabium (Keilin).

The submentum is represented by a narrow transverse strip in the eucephalous groups of crane-flies, being well shown in Ptychoptera. The mentum is the usually chitinized anterior-ventral plate of the capsule. In Ptychoptera it is margined anteriorly with about twenty comblike teeth. In Bittacomorpha it is more or less distinctly bilobed, but is untoothed. In the generalized Tipulidae it is indistinctly divided into an outer plate and, immediately dorsad of this and closely applied to or fused with it, an inner plate. The outer plate furnishes the apical median tooth of the mentum and in some cases an additional tooth on either side. The inner plate adds a varying number of teeth to the mental plate, from two in Epiphragma to as many as ten or twelve in some species of Limnobia. The chitinized plate is completely divided medially in some Eriopterini (Molophilus and some Erioptera), in the Pediciini, and in some Hexatomini (Pseudolimnophila). In this case, each half is

directly continuous with the ventral bars of the head capsule. In the Limnophilaria the mentum is represented by a narrow, transverse, chitinized bar, which is delicately grooved with parallel lines. The mentum is lacking in chitinized parts, or apparently so, in many Eriopterini and in the higher Hexatomini.

Directly behind the mentum is the prementum, rarely prominent and bearing the two small palpi when they are preserved, as in the Ptychopteridae. The hypopharynx lies immediately dorsad of the prementum. In the Ptychopteridae this is an enlarged, two-horned, fleshy lobe which is difficult to study. In the Tipulidae the generalized condition, such as occurs in the Limnobiini and the lower Hexatomini, consists of two collar-like chitinized plates whose anterior margins bear from ten to fifteen or more teeth. In the Tipulini this plate is narrow, with the anterior margin few-toothed, there usually being five or in some cases six teeth. In the Pediciini the hypopharynx is labriform; in many Eriopterini it is cushion-shaped and covered with numerous blunt setae.

The antennae.— The antennae are borne on the anterior lateral margin of the capsule, laterad of the labrum. They are one- or two-segmented, and in most cases have one or more apical papillae. De Meijere and others hold that the principal apical papilla constitutes an additional antennal segment. In some cases, however, as in Ula for example, two or even more papillae are found which are very similar to one another except for slight degrees of size. It is difficult in such cases to hold any one of these papillae as a true segment. The writer prefers to consider them as apical sensory papillae, and they are so treated in this paper.

The primitive antennae are not greatly elongated, and are usually short-cylindrical or subglobular (Ula). An auditory plate, circular in outline and lying on the face of the basal segment, is almost always present. The apical papilla in the Limnophilaria and the Eriopterini is egg-shaped, or oval, and is delicately sculptured by a network of apparently impressed lines. In many species, as for example those of the higher Hexatomini, the apical papillae are very long, tapering to the tips. In many Limnobiini, as for example Limnobia, and in many species of Tipula and related forms, the apical papilla is button-shaped, or disklike, and is often very reduced.

The mandible.— In the primitive type, such as occurs in the eucephalous groups and in the generalized Tipulidae, the mandible is rather com-

plicated, usually having a considerable number of teeth on the cutting edge and a distinct sub-basal arm (prŏstheca) or prostheeal tuft of hairs. At the same time there are usually one or more setae on the outside of the mandible, near the "heel," or base, of the scrobal region. In the generalized tipulid type there are two apical teeth and two rows of cutting teeth. In other cases, as in the Limnobiini, there are but a single dorsal tooth, a single apical tooth, and a varying number of cutting teeth on the ventral face; in some species of Limnobia the number of teeth in the ventral cutting row is six or seven. In the Tipulini the mandible is often reduced in size (as in Tanyptera), there being but a single dorsal and a single ventral tooth in addition to the apical point; the prostheca, however, is usually well developed. In the Eriopterini but one row of teeth, the ventral, is strongly developed. In the Pediciini and the higher Hexatomini, the mandible is elongate and sickle-shaped, with the few teeth on the cutting edge at about midlength. In Ulomorpha the mandible is hinged at about midlength, the basal part being hollowed out on the inner face to receive the blade in a position of rest.

The maxillae.— The maxillae are usually of simple form. In the generalized types, such as the eucephalous families and the lower groups of the subfamilies of Tipulidae, they consist of a large and distinct transversely triangular cardo, a conspicuous stipes, and distinct inner and outer apical lobes. In the Pediciini the lobes are separate in the supposed Adelphomyia larva but are fused together in the highest types (Dicranota). In the Hexatomini the lobes are reduced to a single long, flattened blade. The outer and inner lobes are usually densely hairy, especially at the tip and on the inner face of the latter. The palpus is uni-articulate and antenniform in the generalized forms, is short-cylindrical with a varying number of tiny sense pegs at the apex, and bears on its face a circular auditory plate similar to that of the antenna. The armature of the inner lobes is varied, in some species being provided with stiff, comblike setae, or projections.

The pupa

General features

The pupa of the crane-fly is of the so-called "free," or "mummy," type. In only a few cases does the larval skin adhere to the end of the abdomen (Dactylolabis, Cylindrotoma, and some other forms.) The head is usually small, and is ventral in position. Immediately behind the

head on the pronotum are the two breathing horns, which are variously developed in the different tribes and genera and furnish invaluable bases for classification. The leg sheaths usually far exceed the short or but moderately elongate wing sheaths. The abdominal segments are often provided with a subterminal armature of stiff setae, or spines. At the posterior end of the body, the last two segments (cauda) are variously modified to inclose the sexual organs of the adult flies.

The head

The head is usually small and flattened, occupying the anterior ventral part of the body. The eyes differ in size in the various groups, in some (Erioptera, Elephantomyia) being larger in the male than in the female; in the male sex they are approximated on the median line above or beneath.

The front between the eyes is usually narrowed behind, delimited by the inner margin of the compound eye, narrowed at the posterior end, and bluntly rounded or pointed at the apex. This part is described herein as the *labrum*, or *labral sheath*. It contains the fronto-clypeus and the labrum of the imago. At its tip it bears two more or less divergent lobes, these being in some cases closely approximated so as to appear as a single lobe; these are herein termed the *labial lobes* or *sheaths*, and they contain the so-called paraglossae of the adult fly.

On either side of the labral sheath, and usually divergent and lying along the posterior margin of its face, are the sheaths of the maxillary palpi, which in most cases extend beyond the knee joint of the fore legs. In almost all the Limnobiinae these are short and stout and almost straight, but in the majority of the tipuline forms they are curved at their tips, which in most species are actually recurved and offer an easy means of distinguishing members of this subfamily. In many of the Limnobiini the margins of the cheeks project as flattened ledges overlying the joint of the fore legs.

The antennae arise from above or between the eyes and bend laterad and thence caudad around the eyes, in some forms, such as Elephantomyia and the males of other species, lying across the face of the eyes. The antennae usually end just beyond the roots of the wings, but in the males of some species (Eriocera) they extend beyond the tips of the wings. The basal segments (scape) of the antennal sheath are often armed with

spines or tubercles, and very often the organ is angulated at the end of each segment of the adult antenna inside.

At its vertex, between or just dorsad of the antennal bases, the head may bear a crest which is usually bilobed and setiferous. In some species this cephalic crest is quadrituberculate, there being a smaller secondary crest behind or before the primary one. In the Tipulini the crest is very inconspicuous and but weakly setiferous. In most of the Limnobiini it is lacking or nearly so.

The head may be variously armed with spines, tubercles, or setae; in *Eriocera spinosa*, for example, there are spines or strong tubercles on the antennal scape, on the clypeal region, and even on the face of the eye. In some cases there are setae on the front between the eyes, on the clypeus, and on the cheek.

The thorax

The pronotum of the thorax is small. The ventral part is closely applied to the head and often has small setiferous tubercles close to the breathing horns. The pronotal breathing horns are variously developed in the different tribes and genera, and are discussed here in general terms only.

Many species are propneustic, the pronotal horns alone being functional. Other species (in Hexatomini and Eriopterini) are peripneustic, the second to the seventh abdominal segments being provided with functional lateral spiracles in addition to the breathing horns; other pupae have lateral abdominal spiracles, but in most cases they are merely vestigial. Some pupae are amphipneustic, there being in addition to the breathing horns a conspicuous pair of spiracles on the dorsum of the eighth abdominal segment (Rhamphidia, Ula, Epiphragma; in the typical species of Limnobia these are present but they are small and are probably nonfunctional).

In the Ptychopteridae the breathing horns are very unequally developed, one being enormously elongated and filiform while the other is abortive. In some Tipulini (Longurio, Prionocera, Tipulodina) the horns are likewise greatly elongated, but in these cases they are shorter than the body and are approximately subequal in size, or at least are not so disproportionately unequal.

In the Limnobiini the breathing horns are usually stout and broad, in the typical Limnobaria (Limnobia, Dicranomyia) being subquadrate,

subcircular, or even broader than long. In Elliptera they are earlike and very large. In Antocha a unique condition is found, in that the apparatus is divided into eight stout filaments. In the Eriopterini and the Hexatomini the horns are usually long and cylindrical or slightly flattened, and straight or but slightly curved. There are numerous deviations from type, however. In Gnophomyia and some species of Gonomyia (*alexanderi* and *kansensis*, for example), the horns are trumpet-shaped; in *Gonomyia sulphurella* they are compressed and flattened into fanlike structures. In several widely separated paludicolous genera, such as Ulomorpha, Pseudolimnophila, and Prionocera, the breathing horns are split at their tips into two conspicuous flaps with fimbriate margins, an obvious adaptation to an existence in mud. Often the breathing horns are very small (as in Elephantomyia, Teucholabis, and Trichocera) or even microscopic (Dicranoptycha). *Limnophila hyalipennis* (Zett.) is described by Beling (1886:198–199) as lacking the breathing horns, but this is presumably an error of observation which may be due to a defect in the material studied, or possibly the horns are sessile or reduced as in Dicranoptycha. In some species (Erioptera, Eriocera) the horns are stout at the base but taper rapidly to the acute points. In many Pediciini the tips of the horns are expanded and usually obliquely truncated, with a row of breathing pores around the margin. The tipuline breathing horns are remarkably uniform in general structure, being usually elongated cylindrical in shape, of moderate length, and with the tips slightly expanded. The most conspicuous deviations from type are the short, flattened, and somewhat clavate horns of Tanyptera.

The thoracic mesonotum is very convex, or gibbous in many species (Limnobiini and some Hexatomini). In other species it is declivitous, with a high transverse crest (Eriopterini). This crest may be armed with numerous small spines (Helobia); from two to four powerful hooks (Molophilus, some species of Ormosia, some species of Erioptera, Teucholabis); from six to eight tubercles set with stiff bristles (Gonomyia); or abundant small setiferous tubercles on either side of the median line, these being less conspicuous along the shoulder (most species of Ormosia and of Erioptera). In *Eriocera longicornis* there is a median spine or tubercle on the scutellum. In some Cylindrotominae the metanotum bears spines. The extreme lateral or ventral margin is produced into a blunt or somewhat pointed angle just above the wing

root; this is usually armed with from one to three setae. Various other setae usually occur on the mesonotum.

The leg sheaths lie along the ventral side of the pupa. There is, in the various groups, a considerable difference in the length of the sheaths, their position, and the relative arrangement of the ends of the tarsal segments. In the Bittacomorphinae, the fore legs overlie the middle legs. In the Rhyphidae the fore legs overlie the middle pair, which, in turn, overlie the hind legs. In the Ptychopterinae and in the Tipulidae, all three pairs of sheaths lie parallel along the midventral area, those of the hind legs being outermost along the wing sheaths, and those of the fore legs being on the inside and contiguous. In Gnophomyia the leg sheaths are very short, extending but little beyond the wing tips and reaching only the end of the second abdominal segment. In other crane-flies they are longer, in some species reaching the end of the fifth abdominal segment. Very often the tips of the tarsi are on a level. In the Limnobiini the hind tarsi are usually a little shorter, and the fore tarsi are a little longer, so that the ends of the sheaths form a blunt V. In the Eriopterini the middle legs are usually (except in Gnophomyia) much shorter than the other legs; in Helobia, moreover, the hind legs are conspicuously longer than the fore legs, so that all three sets end at different levels. A somewhat similar and parallel development is found in the tipuline forms.

The wing sheaths are moderately broad, usually ending opposite or a little beyond the apex of the second abdominal segment. The venation of the various species often shows clearly and with little distortion on the wing pad, and in such cases it is of very great help in locating certain genera. Species with a heavy pattern in the adult wings, such as those of the genera Discobola and Epiphragma, show this pattern on the wing pad in the older pupae, and this helps to confirm their identity.

The abdomen

The abdomen consists of apparently nine segments, the last two being closely approximated or fused to form the cauda. The segments are usually plainly divided into a broad dorsal (tergal) and ventral (sternal) region, and a much narrower and more restricted lateral (pleural) area. The segments beyond the first are variously subdivided into rings, or annuli, by false constrictions, there being usually one, but in some cases

two or more, basal rings and a much broader posterior ring. The segments are variously armed with setae, or spines. In the Limnobiini and some Hexatomini these occur on the basal annulus, and consist of a transverse welt which is margined (as in Antocha and Elliptera) or covered with abundant microscopic chitinized points. In some Pediciini the setae occupy both the basal and the posterior rings of the intermediate abdominal segments. In the Eriopterini and most Hexatomini, as well as in the tipuline forms, the setae occur on the posterior ring, just before the caudal margin, and consist of a single transverse row of small spines. In the Cylindrotominae the segments are often armed with prominent elongate body projections (Liogma, Triogma). In Phalacrocera elongate lobes are confined to the posterior segments of the abdomen. In the Ptychopteridae the segments are densely covered with transverse rows of long tubercles which are replaced by chitinized plates near the posterior margin of the segments. In Bittacomorpha these tubercles are stellate at their tips.

The dorsum of the cauda in most crane-flies is armed with four, five, or six conspicuous lobes which are often spinous at or near their tips. These represent the lobes that surround the spiracular disk of the larva, and their number generally corresponds to the larval condition. Thus, in the Ptychopteridae there is a single lobe, in the Pediciini there are two, and in the Hexatomini and the Eriopterini there are four or five. In the Tipulinae there are often but four evident lobes, the dorsal pair of the larva not being represented. In some generalized groups, as the Limnobaria, the Rhamphidaria, and others as indicated elsewhere in this paper, the larval spiracles persist in a more or less functional condition.

Abdominal spiracles.— In the Eriopterini and the Hexatomini there is a distinct and apparently functional spiracle on each pleurite of the second to the seventh abdominal segments, located near the base of the posterior ring. In the Eriopterini these spiracles are small and, in the cast pupal skin, appear tubular or elongate. Smaller vestigial spiracles are evident in most genera of the Tipulidae.

As has been mentioned earlier in this paper, in certain primitive genera of Tipulidae — such as Rhamphidia, Ula, Epiphragma, and to a lesser extent those of Limnobaria — there is a pair of rather large spiracles on the dorsum of the eighth segment. In *Dactylolabis cubitalis* the lateral

abdominal spiracles are protuberant, notably the pair on the second segment.

The genitalia.— The genital sheaths conceal the adult organs within. In the male the valves are usually subequal or the sternal valves are a little the longer. In the female the sheaths, or acidothecae, of the ovipositor usually have the dorsal valves considerably longer than the sternal valves and distinctly upturned at their tips. In the few groups with fleshy ovipositors, the female cauda is very difficult to distinguish from the cauda of the male. The valves are variously armed with spines or lobes, at or before the tips.

INTERNAL MORPHOLOGY

The internal morphology and anatomy of the crane-fly larva are here considered in general terms only. The two genera that have been studied in greatest detail by the writer are Eriocera and Antocha. The most important literature on the various systems of the body is cited in order to make reference to it more easily available.

The digestive system

The most important literature on the digestive system is as follows:

Ptychoptera. Grobben, 1876; Van Gehuchten, 1890.
Chionea. Brauer, Egger, and Frauenfeld, 1854:613–614, pl. 11, fig. 4.
Dicranota. Miall, 1893:242–245.
Phalacrocera. Miall and Shelford, 1897:347–351; Bengtsson, 1897.
Ctenophora. Anthon, 1908:546–551, figs. 12–35.
Holorusia. Kellogg, 1901 a; Comstock and Kellogg, 1904:56–57.

Herbivorous larvae (*Tipula, Holorusia, Ctenophora, Phalacrocera*)

In the larva of herbivorous species the alimentary canal extends the length of the body as an almost straight tube inclosed by the coiled, perforated sheets of adipose tissue. The esophagus is slender, opening into the hypopharynx. The proventriculus has a large esophageal invagination at its anterior end. The ventriculus has at its anterior end four elongated ventricular caeca, these being of two distinct lengths in pairs (didynamous) in Ctenophora, and all four alike in Holorusia. In Ctenophora there are four small, pocket-like gastric caeca near the posterior end of the ventriculus, which are not mentioned as occurring in Holorusia. At the juncture of the ventriculus and the small intestine are the four

coiled malpighian tubules. Behind the ventriculus lies the small intestine, with a caliber much smaller than that of the ventriculus. At the union of the large and the small intestine is a prominent diverticulum of very large size (in Ctenophora three times as large as in Holorusia). The large intestine gradually dilates behind to form the rectum.

Phalacrocera has the ventriculus without caeca and the hind intestine without a diverticulum, altho it is decidedly a herbivorous genus. The condition in Chionea is almost the same. In Phalacrocera, and probably in most other larvae, a peritrophic membrane (a secretion of the epithelium which incases the food and keeps it from direct contact with the epithelium) is present.

There are four malpighian tubules in all the Tipulidae that have been thoroly studied (Chionea, Eriocera, Dicranota, Phalacrocera, Ctenophora, Holorusia, Tipula, and a few others). In the Rhyphidae, likewise, there are four tubules in both the larval and adult stages. In the Ptychopteridae, however, there are five tubules, as in the Culicidae, the Psychodidae, and related families. This might indicate some basis for placing the Ptychopteridae in close proximity to the Culicidae, as has been done by Lameere (1906).

The salivary glands consist of two large coiled tubules which pass into a collecting duct and unite to form the common collecting duct that opens at the base of the hypopharynx.

Carnivorous larvae (*Dicranota, Eriocera*)

The alimentary canal in the carnivorous type of crane-flies is a short, straight tube, with a minimum of appendages such as caeca and diverticula. In Eriocera the esophagus is very long, and the ventriculus is short and without caeca. The malpighian tubules are yellow at their origin, soon passing into an orange-brown color. The intestine is short and straight, without a diverticulum.

The salivary glands in the newly killed larva of *Eriocera spinosa* are very conspicuous by their opalescent color, which persists for a day or more after death. These glands consist of two elongate-oval or cylindrical glands, of the opalescent color just mentioned. From the anterior end of each of these glands passes the long, slender, salivary collecting duct, which unites with its fellow to form a common duct opening at the mouth cavity. From the caudal end of each gland is a flattened, almost hyaline,

elongate lobe which is indistinctly pseudo-segmented, in its posterior part being in intimate connection with the abundant fat tissue.

Respiration and circulation

The most important literature on the respiratory and circulatory organs is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893: 245–248.
Phalacrocera. Miall and Shelford, 1897: 351–356.
Liogma. Müggenberg, 1901.
Ctenophora. Anthon, 1908: 551–554.
Holorusia. Kellogg, 1901 a; Comstock and Kellogg, 1904: 57–58, 60.
Tipula maxima. Brown, 1910.
Tipulinae, Hexatomini (especially *Tipula paludosa* and *Limnophila punctata*). Gerbig, 1913.
General articles. De Meijere, 1895; Viallanes, 1880.

The most important works on the structure of the tracheal system with special reference to the mechanics of the spiracles, are those by Müggenberg (1901), De Meijere (1895, 1902, 1916), Brown (1910), and Gerbig (1913). Miall and Shelford (1897: 351–356) discuss in much detail the structure of the heart in Phalacrocera.

In *Eriocera spinosa*, which may be considered as typical for this group of crane-flies, there are two principal tracheal trunks which lie in a dorsal position and run almost the length of the body. They are connected across by a very delicate, unbranched, simple, tracheal commissure, and send off branches laterally to supply the various organs of the body. Near the posterior end of the body they are approximated, and just in front of the spiracles they expand into the tracheal chamber. Directly cephalad of this chamber the first lateral branch passes off, numbering from the posterior end forward. Branches 2 to 8 are large and much forked. Just after leaving the main tracheal trunks, each of these sends off a ventral branch which supplies the alimentary canal and the fat tissue. Branch 3 supplies the region of the malpighian tubules; branch 4, the posterior part of the stomach; branch 5, the anterior part of the stomach; branches 6 to 8, the esophageal region — branch 6 supplying the proventriculus, branch 7 and part of branch 8 the esophagus, and the remainder of branch 8 the pharyngeal region.

The main part of each lateral branch continues laterad, at its first (anterior) fork sending a branch forward to the next branch, so as to

form a complete but much-branched lateral trachea. The branches are very diffuse and abundant and the skin is well supplied. As already stated, the cross-commissures are very delicate and are unbranched or nearly so, the dorsal regions of the body being supplied by branches from the lateral supply.

The condition of the tracheae in Antocha, the only apneustic crane-fly larva among the species here considered, may be outlined as follows:

The usual two principal trunks are present, joined across on each segment by delicate cross-commissures which send off two approximated branches except on the eighth segment. Laterad and ventrad of the principal trunks are the delicate lateral tracheae. These are joined to the main trunks by fine branches inserted about midway between the dorsal commissures, toward the posterior end of the body lying nearer the posterior commissure than the anterior one.

At the ninth segment each trunk sends off a branch from its proximal side, these branches being connected by a long commissure and supplying the posterior pair of gills. The commissure is about as long as that part of the branch between it and the trunk. Immediately caudad of, or just at, the fork, but on the ventral side, a subequal branch passes into the anterior gills; at the same point the delicate lateral tracheal trunk finally ends in the main trunk. Caudad of this triple forking the main trunk gradually widens out into a cylindrical structure which is truncated apically, at the tip passing out into two small elongate branches, near the base with about three delicate branches, two being dorsal in position and one more lateral. All of these tracheae, to the gills and to the caudal lobes, send off many branched capillaries at frequent intervals, and the caudal lobes unquestionably function as tracheal gills.

A comparison of Antocha with Dicranota as described and figured by Miall (1893:245–248) shows, in the latter, distinct spiracles and the gills similar but much smaller. The tracheal arrangement differs in that a single branch on either side supplies both gills of that side, while the caudal lobes are tracheated by a branch that leaves the main trunk close to the spiracles. (Plate XII, 2 and 3.)

The arrangement of the tracheae at the base of the wing pad is described and figured for Bittacomorpha by Dr. Chapman in Comstock's *The Wings of Insects* (1918:36–37).

The nervous system

The most important literature on the nervous system is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893: 241.
Phalacrocera. Miall and Shelford, 1897: 356; Bengtsson, 1897.
Ctenophora. Anthon, 1908: 556–557.
Holorusia. Comstock and Kellogg, 1904: 58–59.

In Holorusia the brain, or supra-esophageal ganglion, is composed of two principal lobes united posteriorly and lying above the esophagus. Beneath the brain and on the under side of the esophagus lies the subesophageal ganglion, which is connected with the anterior end of the brain lobe by the circum-esophageal commissures. The above-named organs form a complete ring, or collar, around the alimentary canal. The ventral nervous system leads backward from the subesophageal ganglion on the ventral surface of the body wall. In the thorax there are four closely approximated ganglia representing the thoracic and the first abdominal segments. Beyond these and located in the abdomen are six abdominal ganglia. The ganglia send off four large nerve trunks.

The condition is similar in Ctenophora and in Tipula, there being seven abdominal ganglia, of which the first is located in the thorax and the last six in the abdomen. In Phalacrocera there are eight abdominal ganglia, the first being usually found in the first abdominal segment and the eighth in segment 10. The head ganglia are all independent of one another, not fused into a complex. The longitudinal commissures between the first five ventral ganglia are double, and those between the eight abdominal ganglia are simple (Bengtsson). In Dicranota there are likewise eight abdominal ganglia, the first being located in the first abdominal segment and the others in segments 5 to 10, there being two close together in the tenth segment.

The reproductive system

The most important literature on the reproductive system is as follows:

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893: 248.
Phalacrocera. Miall and Shelford, 1897: 356–357.
Holorusia. Comstock and Kellogg, 1904: 58.

The reproductive organs appear early in the larval development. In Dicranota the testes lie in the ninth segment and form elongate capsules.

when sufficiently advanced giving off the vasa deferentia from the inner side of the hinder end. Even in larvae not fully matured, Miall found ripe spermatazoa mixed with spermatoblasts. No division of the testes into follicles is apparent. In Phalacrocera, also, ripe spermatazoa may be found in the older larvae.

In Phalacrocera the ovaries form a pair of cylindrical bodies tapering to each end, lying on either side of the beginning of the intestine. The ovaries are very peculiar in structure, seeming to be adapted to the almost simultaneous discharge of all the eggs.

The muscular system

The most important literature on the muscular system is as follows:

Body musculation

Ptychoptera. Grobben, 1876.
Dicranota. Miall, 1893:241.
Ctenophora. Anthon, 1908:545.
Holorusia. Comstock and Kellogg, 1904:59–60.

Musculation of the mouth parts

Phalacrocera. Bengtsson, 1897.

The fat bodies, or adipose tissue

The most important literature on the adipose tissue is as follows:

Dicranota. Miall, 1893:241–242.
Ctenophora. Anthon, 1908:554.
Holorusia. Comstock and Kellogg, 1904:56.

The imaginal disks, or histoblasts

The most important literature on the imaginal disks is as follows:

Phalacrocera. Miall and Shelford, 1897:357–358.
Ctenophora. Anthon, 1908:555.
Holorusia. Kellogg, 1901 b; Comstock and Kellogg, 1904:61.

PHYLOGENY

The origin and phylogenetic development of the various groups of crane-flies is still largely problematical. The evidence supplied by the adult flies of the most generalized living groups points to an ancestor which in many respects resembled the recent Mecoptera, or scorpion

flies. That this resemblance is presumably not fundamental is suggested by the immature stages of these same generalized forms, which show but few features that can be reconciled with those of a panorpid-like ancestor. Unfortunately the fossil record helps but little. At the beginning of the Tertiaries, crane-flies were already numerous both in species and in individuals, but in most cases they are clearly referable to existing genera. It is evident, then, that the investigator must go still further back for his evidence, and the fossil crane-flies of the Upper Mesozoic are, unfortunately, still largely unavailable. The phylogenetic development of the group may be considered from two standpoints, the geological record and comparative morphology.

THE GEOLOGICAL RECORD

The most important works on fossil crane-flies are those of Loew (1850), Scudder (1894), Handlirsch (1906–08, and 1910, a and b), Meunier (1906), and Cockerell (1910, 1913, 1916, and 1917, a and b). The writer is indebted to Professor Cockerell for assistance in determining the age of many of the fossil-bearing beds. Excellent accounts of the various deposits may be found in Cockerell (1913) and in Tillyard (1917).

The Tipuloidea, representing the superfamily of crane-flies, is herein considered as being constituted of six families, of which two, the Eoptychopteridae and the Architipulidae, did not survive the Mesozoic period. The Eoptychopteridae are known only from the Mecklenburg Lias (lowest Jurassic), and include but three monotypic genera. The Architipulidae are known from the same formation and include eight species arranged in three genera. The other four families contain recent forms and are included in this paper.

The North American Eocene and Miocene, as represented by the White River and Green River beds and the Florissant shales, respectively, give evidence of having had a northern fauna, especially in the Eocene. This is well shown by the great development of the Cylindrotominae, which in the White River basin almost dominated the crane-fly fauna during the Eocene. It seems probable, moreover, that the group was forced into colder regions of the globe during the Oligocene, when the tropical element reached far to the north. No group of crane-flies that can be considered as being tropical has yet been found in the Florissant. On the other hand, the European Oligocene, as shown by the Gurnet Bay beds

and the lower Oligocene Baltic amber, has a considerable tropical element apparent — as, for instance, Styringomyia, found in both formations, and Trentepohlia, Polymera, and Brachypremna, the last two being amber records. In connection with these two last-named genera, as fossils known only from the Baltic amber, it should be noted that each is found living to-day only in America, where they are confined to the austral and tropical regions.

The Tanyderidae are represented by the Oligocene Macrochile (amber) and Etoptychoptera. At present this is still a very small group, including but two genera and nine species.

The Ptychopteridae include a Ptychoptera from the Bohemian Krottensee (probably upper Oligocene) and a Bittacomorpha from the Florissant.

The Rhyphidae (Trichocerinae) are represented by two species from the Baltic amber and one or two additional species from the Miocene.

The Tipulidae may be considered in general terms only. But one tipulid is listed by Handlirsch as being known from the Mesozoic. In the earliest Tertiaries, however, a variety of species is found in this family which almost parallels their recent development.

The Limnobiini first appeared in the Eocene (Dicranomyia, Geranomyia). In the lower Oligocene, numerous species of Dicranomyia and Rhipidia occurred. In the Miocene, Dicranomyia was common, tho probably not so rich in species as at present. Rhamphidia is found in amber, and Antocha has been described from the Florissant Miocene by Scudder; the latter record, however, seems very doubtful to the writer, judging from Scudder's figure and description.

The Hexatomini are represented by Ula, Limnophila, Eriocera, and Polymera in amber, and by Limnophila in the Florissant shales.

There is no record of the Pediciini being preserved as fossils.

The Eriopterini are well represented in the Baltic amber by Erioptera, Gnophomyia, Gonomyia, and related genera, and also in the Miocene by Gonomyia, Cladura, and others. Toxorhina, an apparent relative of Elephantomyia, occurs in the Baltic amber.

The Styringomyiini are represented by the only living genus, Styringomyia, a fly of uncertain affinities, in the Gurnet Bay Oligocene (Cockerell, 1917c and 1919) and in amber, reappearing in the Pleistocene African copal.

The dominance of the Cylindrotominae (genus Cyttaromyia) in the Eocene and Miocene of the North American fauna has already been mentioned. No records of this group from the European Oligocene are available. The recent species of the subfamily are practically all forms belonging to cold, temperate regions, the few Oriental species of Stibadocera coming from mountains at considerable altitudes.

The Tipulinae have been found as far back as the Mesozoic, but the records are not entirely satisfactory. In the lowermost Tertiaries, however, undoubted tipuline forms occur. Species occur in the Green River shales of Colorado (Eocene). The group was well represented in the Oligocene (Baltic amber, Tulameen beds of British Columbia, Krottensee, and Gurnet Bay), and was very common in the Miocene (Radoboj, and especially in the Florissant of Colorado, where some twenty-five species of Tipula and closely allied genera or subgenera have been described by Scudder and Cockerell).

Tipulidae of the Pleistocene are not numerous, only a few having been made known from the refuse of lake dwellings in England (Dicaera, apparently related to Ctenophora), and in the African copal, including such genera as Styringomyia, Elephantomyia, and Toxorhina.

COMPARATIVE MORPHOLOGY

The morphology of the various stages of crane-flies has been detailed elsewhere in this paper and need not be repeated here.

PHYLOGENETIC CONSIDERATIONS

The eucephalous familes of crane-flies are undoubtedly lower, phylogenetically, than the Tipulidae, and the latter have been derived from the former. The generalized type recurs in all three subfamilies of the Tipulidae, and it is uncertain which of these three should be placed lowermost. Presumably all three groups arose from an immediate common ancestor, or the Tipulinae and the Limnobiinae arose from one point of the tree, the Cylindrotominae developing from the limnobiine stem at a somewhat later period. The accompanying phylogenetic tree (Plate XII, 4) graphically illustrates this apparent evolution of the group. The Limnobiini show but little deviation from the fundamental type. From the level of the lowermost Hexatomini (Ula and Epiphragma), in close proximity to the Limnobiini, the remaining groups of crane-flies can be

derived — the Pediciini and the Eriopterini on the one hand, the hexatomine divisions on the other. The highest levels of development of their respective types are apparently Diotrepha (Limnobiini), Dicranota (Pediciini), Gonomyia (Eriopterini), and Hexatoma (Hexatomini).

The immature stages of the Tipulidae of the antipodal regions (Australia and Chile) are entirely unknown, and their discovery may bring to light striking novelties that may well upset the present ideas of classification. The largest remaining gaps in the present knowledge of the Nearctic fauna relate to the genera Atarba, Toxorhina, Cryptolabis, Phyllolabis, and Megistocera, but it is not expected that any major groups will have to be created for their reception.

LIFE HISTORIES OF CRANE-FLIES, WITH KEYS AND DESCRIPTIONS OF THE SPECIES

Various classifications and arrangements of Diptera have been proposed in the past, and the principal evolutionary changes in the entomologist's conception of classification are herein indicated.

The groupings in the superfamily Tipuloidea have been very diverse. Brauer (1883) separated the eucephalous families from the Tipulidae (Polyneura). Osten Sacken (1893) placed the Tipulidae in the *Nemocera vera*, the Rhyphidae in the *Nemocera anomala*. Coquillett (in Howard, 1912:85–86) included the Tipulidae in his superfamily Tipuloidea, but separated the Rhyphidae, placing the latter in Bibionoidea. Lameere (1906) gave a classification that had little basis in fact, the Rhyphidae being considered by him as Brachycera and the Ptychopteridae being placed with the Culicidae. Knab (1915), working on the respiratory systems of the larvae, demonstrated the hitherto unnatural groupings of the families of the Nemocera, and arranged the crane-fly families, along with a few others, in the group Polyneura, a group coordinate in rank with the previous conception of the Nematocera. The latest grouping, that of Malloch (1915–17 b), was based on a broad knowledge of both the adult flies and the immature stages; and here, for the first time, one gets the true conception of the superfamily limits — the inclusion of the Ptychopteridae, the Tipulidae, and the Rhyphidae in a single major group. Malloch's arrangement is herein adopted, with the following exceptions: (1) the Limnobiidae are not held as constituting a separate family, but are united with the Tipulidae; (2) the family Tanyderidae has been

erected, to include the generalized Tanyderina which have hitherto been placed with the Ptychopteridae.

The immature stages of the four families of the Tipuloidea are readily separable. The larvae of the Tipulidae can be confused only with those of certain low brachycerous forms, as, for example, the Leptidae. In the Brachycera the mandibles work vertically and parallel to each other; in the Nematocera, including the Tipuloidea, they operate transversely or obliquely against the teeth of the mentum and the hypopharynx. The presence of fleshy lobes surrounding the spiracular disk is a character possessed by almost all Tipulidae. The larvae of a few groups of brachycerous Diptera, such as certain Leptidae, Sciomyzidae, and other families, possess entirely similar caudal lobes but are readily recognized by the small and very reduced head capsule.

The eucephalous families of the Tipuloidea may be distinguished by means of the characters indicated in the following keys:

Larvae

1. Body eucephalous, head non-retractile; amphipneustic or metapneustic..............2
   Head incomplete behind, retractile; not amphipneustic..............TIPULIDAE (p. 791)
2. Caudal end of body prolonged into a slender breathing tube; metapneustic..........3
   Caudal end of body not prolonged into a breathing tube; amphipneustic.
   RHYPHIDAE (p. 787)
3. Breathing tube stouter, non-retractile; gills large, pinnately branched; punctures of head multisetose; found in wet decaying wood..............TANYDERIDAE, supp. (p. 769)
   Breathing tube slender, completely or partly retractile; gills slender, cylindrical, unbranched; punctures of head with simple or plumose hairs; found in wet earth.
   PTYCHOPTERIDAE (p. 772)

Pupae

1. One of the pronotal breathing horns greatly elongated, much longer than the body, the other breathing horn very short, abortive. (Family PTYCHOPTERIDAE, p. 772)......2
   Breathing horns short, or, if elongated (some Tipulinae), not longer than the body and the difference in size not so apparent..3
2. Tarsal sheaths lying side by side, parallel......................**Ptychopterinae** (p. 773)
   The fore tarsal sheaths overlying the middle pair, the four middle and hind tarsi the longest, parallel......................................**Bittacomorphinae** (p. 779)
3. Tarsal sheaths overlying one another in pairs......................RHYPHIDAE (p. 787)
   Tarsal sheaths lying side by side..................................TIPULIDAE (p. 791)

The pupae of the Tanyderidae are still unknown.

It is possible that Bittacomorphella (page 779) has short breathing horns; in this case this genus would run down to couplet 3 above, but by the arrangement of the tarsal sheaths it runs out as indicated in couplet 2.

FAMILY **Tanyderidae**

Larva (supposition).— Body eucephalous, metapneustic. Integument smooth, shiny white. Last two segments of abdomen produced into a stout, non-retractile breathing tube, which is distinctly five-lobed at the tip. Tracheal gills two, very large, pinnately branched. Head with scattered punctures, which are multisetose; lateral plates of head united across venter. Mandibles opposed, narrow, tridentate. Maxilla with palpus two-segmented, the outer lobe digitiform, pubescent. Labrum small, semi-circular, with two punctures; clypeus with four punctures.

Pupa.— Unknown.

The Tanyderidae comprise a group of primitive crane-flies including but three recent genera, with ten species. Of these the genus herein considered, Protoplasa, with three known species, is found in the Northern Hemisphere. All that is known concerning the biology of supposed species of this group pertains to *Protoplasa fitchii* and is discussed below.

Genus **Protoplasa** Osten Sacken (Gr. *first* + *to form*)

1859 *Protoplasa* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.
1878 *Idioplasta* O. S. Cat. Dipt. N. Amer., p. 222.

The genus Protoplasa is confined to temperate North America. There are three known species, of which *P. vipio* O. S. and *P. vanduzeei* Alex. are western in their distribution, while *P. fitchii* O. S. is eastern. The general characters of the supposed larva are given above; the detailed account in connection with the species *P. fitchii* follows.

Protoplasa fitchii O. S.

1859 *Protoplasa fitchii* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The remarkable insect *Protoplasa fitchii* is one of the rarest of the local crane-flies. There are scarcely a score of specimens extant in the various collections of the country, most of which are from the mountainous section of North Carolina. The fly has not been reared, but the writer has in his possession a larva that he refers with much confidence to this species. It is one of the most remarkable dipterous larvae that have ever come to the writer's notice, and, whether or not it belongs to Protoplasa, it should certainly be called to the attention of entomologists in the hope that it may some day be bred and its identity confirmed or ascertained. These peculiar dipterous larvae were discovered by H. S. Barber, C. T. Greene, and

R. C. Shannon, on the Potomac River near the mouth of Dead Run, Fairfax County, Virginia. They were found during the latter part of May, 1916. in a much-decayed maple log, where they were associated with the larvae of the syrphid fly, *Temnostoma bombylans* (Fabr.) (Barber, 1913). Greene attempted to rear the larvae procured at this time, but did not succeed. In May, 1917, he sent the writer one of the preserved larvae for study. Later Dr. Viereck was interested in the matter, and on May 27 he procured one fine, healthy larva, which was sent to the writer at Ithaca, New York. It arrived safely on the 29th, and was at once placed in rearing. Unfortunately this larva died the day after it came into the writer's possession, and this remarkable insect still remains unreared. Associated with this larva in the pieces of decaying maple in which it was shipped, were larvae of Temnostoma and a larva and a pupa of the tipulid *Epiphragma solatrix*.

The evidences that this larva is that of Protoplasa are numerous. It belongs, without doubt, to the Nematocera, and the immature stages of all the remaining families of that division have been made known. Many features in this larva point strongly to the condition in other families of crane-flies. The eucephalous condition of the head, and the elongate breathing tube, are suggestive of the Ptychopteridae; the five-lobed spiracular disk, the anal tracheal gills, the metapneustic respiratory system, and other features, are very similar to conditions in certain Tipulidae. However, there are conditions obtaining here that are found nowhere else in the Diptera, so far as is known to the writer, such as the combination of a eucephalous head of primitive organization, a stout, non-retractile breathing tube, the large, pinnately branched anal gills, the multisetose punctures on the head, and the details of structure of the mouth parts. The multisetose punctures are suggestive of the branched or plumose hairs of Ptychoptera, and give a possible hint of the origin and ancestry of this condition in the latter group. The writer cannot but regard it as suggestive that the larvae are found in direct association with those of Epiphragma in saturated decaying wood. He has mentioned in other papers (Alexander, 1910:254, and 1919 d:883, 915) the remarkable superficial resemblance that exists between the adult flies of *Epiphragma fascipennis* and those of Protoplasa, both forms having very handsomely banded wings of a pattern not found in other species in the local fauna.

The only observations on the adult flies that the writer has ever been able to make were in reference to five specimens taken in New York State in 1909 (Alexander, 1910:254). These were swept from rich vegetation along the banks of the Sacandaga River in northeastern New York. The adult flies have never been recorded from the vicinity of Washington, but are regional, since the species ranges thruout the eastern United States as far south as Georgia (in the mountains).

Larva.—Total length, 11.8 mm.
Length excluding breathing tube, 5.6–6 mm.
Length of breathing tube alone, 5.8–6.2 mm.
Length of ninth segment of abdomen (chitinized part of breathing tube), 3.4–3.6 mm.
Length of anal gills, 2–2.1 mm.
Diameter of body, 2.3 mm.

Coloration pure white, head and apical two-thirds of breathing tube pale brown, chitinized. In the living larva there is a transparent, subcircular area on the dorsum of segment 7 thru which the beating of the heart can be clearly seen, but in preserved specimens this area is hard to perceive. (Plate XIII, 5)

Body eucephalous, entirely smooth, shiny, dorsum of segments 2 to 9 each with a transverse group of tiny points. Thorax with the first segment longer than the succeeding two segments taken together, narrowed anteriorly, broader behind; mesothoracic segment about half as long as the first and about twice as long as the very narrow metathorax. Abdominal segments gradually increasing in length to the seventh; segments 8 and 9 abruptly narrowed into a stout, elongate breathing tube which is about equal in length to remainder of body; basal, or proximal, part of tube (segment 8) shorter than terminal part (segment 9) and not chitinized; segment 9 elongate, chitinized, with a deep transverse constriction a short distance before tip; this apical part, and the region just before the constriction, smooth, the remainder of the last segment with numerous delicate transverse wrinkles. Spiracular disk (Plate XIII, 6) surrounded by five lobes, one dorsal, two lateral, and two ventral in position; dorsal lobe the smallest, lateral lobes the broadest; lobes tipped with sharp, chitinized spines, which are continued for a short distance down the outer face of each lobe; fringes of long hairs along margins of lobes; disk with a brownish tinge around spiracles and an elongate-oval median mark between, and slightly below, the spiracular level; inner face of ventral lobes with indistinct, tiny, brown punctures. Spiracles large, separated by a distance about equal to diameter of one. Anal tracheal gills two, one on either side of the base of segment 8, very large and pinnately branched, there being about fifteen branches to each gill; each of these branches constricted into four or five lobules; lobes at their tips broadly obtuse (Plate XIII, 9).

Head short and broad, epicranium chitinized. Across ventral face, the sclerite firmly united by a narrow transverse band; median part densely punctulate, this area delimited laterally and posteriorly by an indistinct curved line. On dorsum, the prefrons conspicuous and the clypeus distinct from the labrum. Head and mouth parts provided with numerous setiferous punctures, each of which is multisetose (from five to eight setae to each puncture). Chaetotaxy of epicranium (Plate XIII, 7) with three lateral groups of long bristles, the

posterior group being the longest and most dorsal in position; on ventral face, four punctures on either side (Plate XIII, 8); prefrontal sclerite apparently lacking setae, but on the epicranium proper, along margin of prefrons, a longitudinal group of six punctures on either side, the anterior pair the longest. Labrum semicircular in outline, outer margin fringed with long, stiff hairs; dorsal surface with two transverse punctures. Clypeus narrowly transverse, with four setiferous punctures in a transverse row. Dorsal median part of epicranium forming a subquadrate lobe whose lateral angles bear brushes of hairs; laterad of these angles a rounded hollow overlapped by a flat, bilobed operculum (this may be some modification of the antennae which should occupy about this position on the head). Mandible elongate, strongly chitinized, tridentate, the apical tooth the longest and more acute than the others, the middle tooth bluntly obtuse; inner posterior angle of mandible produced proximad beneath outer lobe of maxilla into a bluntly rounded lobe; mandible with a group of curved setae on scrobe near base, and a group of longer bristles lying distad and mesad of these setae on dorsal face of mandible. Maxilla with base, in a position of rest, concealed beneath head-chitin; palpus stout, antenniform, two-segmented, the basal segment short and stout, the apical segment much shorter and narrower, with a small, lateral, sensory papilla; outer lobe of maxilla produced cephalad as a stout, digitiform lobe which is densely hairy.

FAMILY Ptychopteridae

Larva.— Body eucephalous, metapneustic, long and slender, the caudal end prolonged into a more or less completely retractile breathing tube bearing the spiracles at the tip. Lobes surrounding spiracular disk indistinct. Anal gills two, elongate-cylindrical, unbranched. Integument with tiny hairs (Ptychoptera), or with slight warty protuberances (Bittacomorpha), or with conspicuous elongate tubercles (Bittacomorphella). Pseudopods on abdominal segments 1 to 3 each bearing a curved claw. Head complete; eyespots distinct. Mandibles opposed. Mentum many-toothed (Ptychopterinae) or merely bilobed (Bittacomorphinae).

Pupa.— Usually with one of the two pronotal breathing horns greatly elongated, much longer than the body (this may not be true in Bittacomorphella); in Ptychoptera and Bittacomorpha it is the right horn that is elongated, the left being degenerated; in Bittacomorphella the right horn is degenerated. Tarsal sheaths all parallel in the Ptychopterinae, the fore pair overlying the middle pair in the Bittacomorphinae. Abdomen covered with setiferous tubercles arranged in transverse rows on tergites and sternites, and more or less in longitudinal rows on pleurites. Cauda with a powerful dorsal median lobe near base of segment 8.

The family Ptychopteridae includes three genera falling in two tribes: the Ptychopterinae including the single genus Ptychoptera, and the Bittacomorphinae including the "phantom crane-flies," Bittacomorpha and Bittacomorphella. The habits of these species are discussed below in connection with the various genera. The following keys separate the subfamilies of the Ptychopteridae:

Larvae

Mentum with outer margin finely serrated; mandibles with three large outer teeth; pseudopods small; coloration yellow or brown........................**Ptychopterinae** (p. 773)
Mentum bilobed, not toothed; mandibles with a single large outer tooth; pseudopods prominent, each with a conspicuous curved claw; coloration rusty red or black.
Bittacomorphinae (p. 779)

Pupae

All tarsi lying parallel; wing pads with *M* branched.............**Ptychopterinae** (p. 773)
Fore tarsi lying above middle tarsi; wing pads with *M* unbranched.
Bittacomorphinae (p. 779)

The immature stages of this group of flies have long been known, having been investigated by Réaumur (1740), Lyonet (1832), and other early workers. The immature stages of the common American species *Ptychoptera rufocincta* are herein recorded for the first time. The unknown Ptychoptera described by Malloch (1915–17b:240–241) is evidently *P. lenis* O. S. and is here considered as that species.

The most important literature on the Ptychopteridae is as follows:

Ptychoptera paludosa...........	Larva, pupa, general..	Réaumur, 1740, pl. 6.
Ptychoptera paludosa...........	General............	Wesenberg-Lund, 1915:348–351.
Ptychoptera lacustris............	Larva..............	Beling, 1886:171–172.
Ptychoptera contaminata........	Larva, general......	Van Gehuchten, 1890. (Histology of the alimentary canal.)
Ptychoptera albimana...........	General............	Cameron, 1917:65.
Ptychoptera albimana...........	Larva, pupa, general..	Topsent, 1914–16.
Ptychoptera sp. (*lenis* supp.).....	Larva..............	Malloch, 1915–17b:240–241.
Ptychoptera sp.................	General............	Léger and Duboscq, 1909. (Protozoan parasites.)
Ptychoptera sp.................	Larva, general......	Grobben, 1876. (Morphology.)
Ptychoptera sp.................	Larva, general......	De Meijere, 1916:188–191, figs. 14–20. (External morphology.)
Ptychoptera sp.................	General............	Lyonet, 1832.
Bittacomorpha clavipes..........	Larva, pupa, general..	Hart, 1898 [1895]:189–195.
Bittacomorpha clavipes..........	General............	Needham and Betten, 1901:574.
Bittacomorpha clavipes..........	General............	Howard, 1912:95–96.
Bittacomorpha clavipes..........	Larva, pupa........	Malloch, 1915–17b:239–240.
Bittacomorpha clavipes..........	General............	Weston and Turner, 1917:53.

Van der Wulp (1857), Miall (1895), Grünberg (1910), and Brunetti (1912) also give general accounts of the immature stages of Ptychoptera, for the most part taken from the earlier works cited above.

SUBFAMILY **Ptychopterinae**

Genus **Ptychoptera** Meigen (Gr. *fold* + *wing*)

1800 *Liriope* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Ptychoptera* Meig. Illiger's Mag., vol. 2, p. 262.
1856 *Ctenoceria* Rond. Dipt. Ital. Prodr., vol. 1, p. 187.

Larva.— Head oval to subpyriform, broadest behind, narrowed in front, not heavily patterned above; setae of head branched or plumose. Submentum large, usually but a little narrowed posteriorly, the anterior lateral angles slightly produced; mentum broader than long, outer margin with numerous teeth (18–22). Prementum with palpi rather small, lying parallel, densely hairy on outer, or ventral, face. Mandible with three powerful outer teeth and about six smaller inner teeth. Maxilla with the cardines elongate-triangular, with three setiferous punctures; maxillary palpi antenniform, cylindrical. Labrum broad, transverse, with dense tufts of hair beneath. Integument almost smooth, without prominent warty elevations. Pseudopods low, with small claws.

Pupa.— Head small, with a reduced cephalic crest. Sheaths of maxillary palpi elongate, the tips projecting around knee joints of fore legs. Leg sheaths with all the tarsi parallel, not overlapping one another. Wing sheaths with media branched. Pronotal breathing horns very unequal, one (usually the right) exceedingly elongate, longer than remainder of body, the other tiny, degenerate. Abdomen set with transverse and longitudinal rows of small setiferous tubercles on the segments.

Ptychoptera is a small genus including sixteen described species, almost all occurring in the Holarctic region, with a few species in India and Formosa. Two species are found in tropical Africa, and another, an undescribed form, in southern South America; hence the genus is probably found thruout the world in countries in the temperate zones, with the probable exception of Australia.

The literature on the immature stages of this genus is summarized under the family account.

Topsent (1914–16) has furnished the best account of any species of the genus Ptychoptera. His observations refer to *Ptychoptera albimana*. The following notes are extracted from Topsent's paper:

The eggs range in number from 520 to 587, averaging 554. They are pale yellow, slightly arcuated, the surface curiously ornamented, the dimensions being 0.825 by 0.264 millimeters. The duration of the egg stage is seven days. The newly hatched larva measures 3.85 millimeters, the respiratory tube 0.99 millimeters. The adult larva measures 77 millimeters, of which the respiratory tube is 20 millimeters. The growth of the larva is rapid. When fifteen days old it measures, when extended, 25 millimeters. When sixty-seven days old, it measures 45 millimeters. The pupal stage is from ten to twelve days, averaging eleven days. There are normally two generations a year.

De Meijere (1916:188–191) gives a critical account of the structure of the larva of a European Ptychoptera. It agrees well with the description of *P. rufocincta* given below, the most conspicuous differences shown by De Meijere's species being as follows: labium with the submentum having the sides straighter; mentum with the anterior margin evenly, but gently, convex, with only eighteen evident teeth. The details of the maxilla,

especially of the setae on the cardines, are not the same. However, the generic characters given above include all the species to which the writer has been able to refer.

Malloch (1915–17 b:240–241) describes and figures an American Ptychoptera which is presumably *P. lenis* O. S. It agrees closely with the other forms in most respects. The author indicates the mentum as having three distinct parts, the median part being projected beyond the level of the lateral parts and having more teeth (eight instead of six). Malloch's specimens were taken in the Yellowstone Park, Wyoming, in August, 1890. From the locality data it is almost certain that the larvae belong to the common *Ptychoptera lenis* of the western United States.

Tonnoir (1919) describes a curious sexual dimorphism in the genus Ptychoptera.

Ptychoptera rufocincta O. S.

1859 *Ptychoptera rufocincta* O. S. Proc. Acad. Nat. Sci. Phila., p. 252.

The species *Ptychoptera rufocincta* is common around wet swales and among open shrubbery. The adult flies are on the wing from May to early July, and again in late August and early September; they may be double-brooded. In appearance they are conspicuously unlike their relatives of the Bittacomorphinae, rather resembling certain large fungus gnats (Mycetophilidae).

The larvae live in situations similar to those frequented by Bittacomorpha, and often occur in the same associations — with larvae of *Limnophila (Lasiomastix) macrocera*, *Pilaria tenuipes*, *P. recondita*, and *Erioptera chlorophylla*, as well as with many Chironomidae, leeches, nematode worms, and mollusks. In appearance they are strikingly different from the larvae of Bittacomorpha, being pale, white or yellowish white, with the body almost smooth, not covered with the dense transverse rows of setiferous tubercles found in Bittacomorpha, and with the pseudopods on the basal abdominal segments poorly developed. The larvae of this species are smaller than those of Bittacomorpha, with the head proportionately much smaller. In structural details, however, they are rather similar to the larvae of Bittacomorpha. The larvae of *Ptychoptera rufocincta* feed on the decaying vegetable matter in their haunts. When fully grown, the pupa forms within the last larval skin, and the elongate pupal spiracle is coiled about the mesothorax, as described

for *Bittacomorpha clavipes* (Hart, 1898 [1895]: 191). Careful breedings of this species in 1913 at Orono, Maine, placed the indoor pupal life at four days and eighteen hours, and that in nature at probably five days — an unusually short pupal duration.

Larva.— Length, when fully grown, 30–32 mm.; when fully extended, about 35 mm. Diameter, 2–2.2 mm.

Head light reddish brown, not marked with darker spots as in Bittacomorpha; body whitish or pale yellow; tomentum short, pale; seventh and eighth segments of abdomen, and breathing tube, light brown.

Body almost smooth, sparsely clothed with short, appressed hairs arranged in indistinct transverse rows, on intermediate segments of body there being about twenty of these rows; body not at all tuberculate, as in Bittacomorpha. Prothoracic segment short, not so long as mesothorax; metathorax nearly as long as preceding two segments combined. (In older larvae that are about to pupate, the right pupal breathing horn may be seen coiled underneath the skin of the mesothorax.) First five abdominal segments swollen posteriorly into a ring that completely surrounds the segments; first three abdominal segments with low, indistinct pseudopods on either side of the median line, each with a small, recurved claw; pseudopods after first pair more widely separated than, and not so well developed as, in the Bittacomorphinae. Abdominal segments 4 and 5 more elongate, swollen posteriorly but not bearing pseudopods; segment 6 narrowed behind, with a few scattered, outspreading hairs; segment 7 narrower than preceding and telescopic within itself, at about two-fifths the length there being a transverse row of long hairs marking the limit of telescoping; when fully extended, segment 7 a little longer than segment 8; segment 8 a little narrower, and telescopic basally into segment 7. (The parts of segments 7 and 8 which are exposed in the retracted condition are brown and subchitinized, and bear scattered, outspread hairs which are most numerous near the caudal end of the exposed part and here form transverse rows; similar rows of sparse, setiferous punctures are on the dorsum of the swellings on the first five abdominal segments.) Breathing tube (segment 9) retractile into segment 8 for about one-fourth its length; when retracted, completely concealing gills. Tracheal gills two, elongate-cylindrical, situated near base of segment 9; in normal position of rest, gills usually projecting about one-half their length beyond end of segment 8. Apex of breathing tube truncated but without well-defined lobes.

Head small, proportionately much smaller than in Bittacomorpha; oval to somewhat pear-shaped; narrow anteriorly, broadened behind, near posterior margin abruptly narrowed. Prefrons broad, conspicuous. (As noted by most earlier writers on the genus Ptychoptera, the head bears numerous punctures with setae which are plumose or have a branched appearance [Plate XV, 20]. The writer has examined numerous specimens under high magnification and is inclined to believe rather that in some cases several bristles arise from a single puncture and are closely approximated basally, altho free distally, and that the plumose appearance is here merely apparent. In other cases, however, actual basal fusion has taken place. The number of free tips from a puncture varies from three to six, five and six being common numbers.) Labrum broad, transverse, on disk two large setiferous punctures bearing branched setae; on either side beneath, conspicuous tufts of long hairs, these tufts continued

obliquely proximad to near median line, where there is a median lobe densely covered with long hairs. Epipharynx small, subquadrate, margin almost transverse, with about seven blunt teeth; sides of organ with long hairs which are directed backward. Labium (Plate XIV, 12) with submentum much narrowed on basal half, sides subparallel, thence expanded so that cephalic end is about twice as wide as caudal end; anterior lateral margins produced into blunt projections; mentum (Plate XV, 17) broadly subquadrate, anterior margin nearly transverse and with from twenty to twenty-two teeth forming an irregular comb. (There is considerable variation in the shape of this comb and in the form of the individual teeth comprising it; usually the median third of the mentum is produced outward beyond the lateral parts, but this condition is not always well-marked; the individual teeth may be blunt or acute. In the specimen shown the normal condition is illustrated; the central lobe includes six teeth, and each lateral part about seven teeth, the lateral teeth being usually a little the larger; in some specimens the median lobe has the teeth very indistinct, while in others there is a conspicuous tendency for the median pair to unite into a single broad tooth.) Prementum pale basally, indistinctly covered with pale papillae; palpi lying close together, subparallel, the lateral parts with short, dense hairs, the ventral face with shorter papillae; each lobe bearing at tip a small, blunt, cylindrical knob which is slightly chitinized. Antenna (Plate XV, 18) short, almost cylindrical but slightly narrowed basally, bearing on truncate apex about five sensory papillae of various diameters, one being much the largest, two others being long and very slender; one of the papillae is bisegmented, the apical part being more slender than the basal part. (De Meijere [1916, fig. 14] shows his European Ptychoptera as having the antennae two-segmented and with the sensory papillae very different from the condition found in *P. rufocincta*.) Mandible (Plate XV, 19) strong and powerful; cutting edge subtriangular, with three large outer teeth and about six or seven small inner ones; of the larger teeth the outermost is the slenderest, the third is the largest and stoutest; small inner teeth subequal in length, the outermost stout, inwardly the teeth becoming more slender; mandible on ventral face near margin with two powerful setae, the posterior one often recurved, the anterior one directed forward. Maxilla (Plate XV, 19) with cardines roughly elongate-triangular, proximal angle acute, ventral face with three large setiferous punctures bearing several bristles of unequal length (the writer has not been able to locate setae on the middle puncture); outer edge of sclerite with a fringe of long hairs, longest at narrow inner end of segment; stipites roughly triangular, with a group of short spines at apex; palpi antenniform, stout, cylindrical, with sensory papillae at tip (one large papilla, about three of medium size, and three or four small ones); outer lobe of maxilla with a small, egg-shaped or subcylindrical, knob at its outer angle, below which the rounded lobe is densely clothed with long, pale hairs; caudad of these, along margin, a row of from six to eight powerful spines and a few long hairs.

Pupa.— Total length, 34.3–40 mm.
Length excluding breathing tube, 14.5–15.8 mm.
Length of breathing tube alone, 19.8–26 mm.
Width of body, d.-s., 1.6–1.7 mm.
Depth, d.-v., 1.7–1.8 mm.

Pronotal breathing horns reddish brown, dark brown at extreme base; thorax, wing sheaths, and leg sheaths dark brown; abdomen whitish, with small tubercles and broad

chitinized apices to segments dark brown. Pupa most readily distinguished from pupa of Bittacomorpha by the venation, the position of the tarsal sheaths, and the short, non-stellate abdominal tubercles. (Plate XIV, 13.)

Anterior cephalic crest small, deeply bilobed by a broad V-shaped notch, the rounded lobules roughened and each terminated by a single long hair. Dorsad of these, two smaller and slenderer, very widely separated, tubercles, each lying just inside antennal sheaths. Antennal bases located on ventral side of head, between eyes; antennae bent dorsad and thence caudad around knee joints of fore legs, the tips lying just outside middle tibiae; apical antennal segments showing distinctly thru sheaths. Sheaths of maxillary palpi elongate, tips curved over knee joints of fore legs. Clypeus smaller and narrower than the conspicuous labium, transversely wrinkled. Labium rectangular, each half with tips obliquely truncated. (Plate XIV, 14.)

Pronotum with lateral ventral angles almost square, each with about two small setae. Breathing horns very unequal in length; the right one greatly elongated, much longer than remainder of body, enlarged at extreme base, the outer part with numerous papillae which are more numerous and more approximated toward end of organ, these papillae lying in a single straight line which makes a long spiral around organ; left breathing horn very small and degenerate, only a little longer than sheath of maxillary palpi, curved, with about a dozen papillae which are closely crowded toward apex of organ. Mesonotum finely and transversely wrinkled, prescutum with a very acute V-shaped dorso-median mark, its apex directed backward; scutal lobes projecting, each with a few tiny hairs. Postnotum with two small tubercles at about two-thirds its length, one on either side of a pale median line. Metanotum short, sheath of halteres extending just beyond base of second abdominal segment. Wing sheaths clearly showing venation, the branched media being characteristic of the genus; wing sheaths extending almost to end of second abdominal segment. Leg sheaths with tips of fore and middle tibiae enlarged, and with inner apical angle of each produced into long points for the long tibial spurs of adult flies. Leg sheaths extending to just before end of third abdominal segment; all six legs lying side by side, not overlapping as in Bittacomorpha (Plate XV, 21).

First abdominal segment chitinized above, apical half with a few weak tubercles. Dorsum of segments 2 to 6 with posterior margins each having a chitinized band set with about twenty-five to thirty setiferous tubercles, the outermost ones being the largest; remainder of dorsum of each segment with irregular transverse rows of scattered tubercles, on narrow, interrupted, chitinized bands; usually one of the bands, at about midlength of segment, broader and more strongly chitinized than the others; these bands obliterated on posterior segments, but caudal band here very wide; about fifteen of these rows on segments 2 and 6, and from twenty to twenty-five rows on segments 3 to 5; these bands not regularly transverse, but anastomosing rather freely, not occupying more than half of abdominal surface; segment 7 with the broad caudal band only; tubercles rather short, with three or four short, irregular spines at tip, these not presenting a stellate appearance as in Bittacomorpha. Abdominal sternites similar to dorsum, tubercles lacking where leg sheaths rest against segments 2 and 3; segments 4 to 6 with transverse rows similar to those of dorsum but weaker; caudal bands on segments 4 to 7 very broad, the caudal margin with tubercles, there being about twenty tubercles on segment 4, the number gradually decreasing to seg-

ment 7, on which there are about fifteen. Abdominal pleurites with tubercles arranged in longitudinal rows, there being about six rows on each of segments 2 to 6, the rows being almost continuous for the whole length of abdomen; tubercles at caudal margin of each segment enlarged and powerful; on segment 6 the rows converging behind into a single powerful tubercle on caudal margin of segment; a similar enlarged tubercle on caudal margin of seventh segment; segment 7 and cauda narrowed. Male cauda (Plate XV, 22) with a prominent dorso-median lobe projecting directly away from the body; dorsal sheaths short, indistinctly bilobed; ventral sheaths very elongate, divergent (Plate XV, 23). Female cauda (Plate XV, 24) with the same prominent dorso-median lobe; acidotheca of ovipositor long, straight, beyond its midlength a blunt, conical tubercle directed laterad and slightly caudad; sternum (Plate XIV, 15) with ventral lobe only about half length of tergal acidothecae, caudal margin with three lobules.

Nepionotype.— Orono, Maine, June 24, 1913.
Neanotype.— With the larval type.
Paratypes.— Both larvae and pupae, June 24 to July 5, 1913.

SUBFAMILY **Bittacomorphinae**

The following keys separate the genera of the subfamily Bittacomorphinae:

Larvae

Size small (total length under 20 mm.); coloration black, breathing tube light yellow; breathing tube entirely retractile; body covered with very long projections which are incased in a black, horny substance; mandibles with an inner comb of teeth. *Bittacomorphella* Alex. (p. 779)

Size larger (total length over 40 mm.); coloration rusty red; body tapering gradually to the long, slender, partly retractile, breathing tube; body covered with transverse rows of shorter, stellate tubercles; mandibles without an inner comb of teeth. *Bittacomorpha* Westw. (p. 783)

Pupae

Size small (length, excluding breathing horn, under 12 mm.); right breathing horn small, degenerate; abdominal tubercles weak, tipped with several strong setae. *Bittacomorphella* Alex. (p. 779)

Size larger (length, excluding breathing horn, over 14 mm.); right breathing horn elongate, filiform, longer than the body; abdominal tubercles strong, elongate, crowned by a circlet of four or five spines and tipped with a setiferous papilla. . .*Bittacomorpha* Westw. (p. 783)

Genus **Bittacomorphella** Alexander (Gr. diminutive of *Bittacomorpha*)

1916 *Bittacomorphella* Alex. Proc. Acad. Nat. Sci. Phila., p. 545.

Larva.— Body short, covered with very prominent projections which are longest on lateral and caudal parts of body. Pseudopods prominent, with very large, curved claws. Breathing tube short, entirely retractile within body. Head subquadrate, the foramen ventral in position; setae of head unbranched. Mandible with an inner comb of teeth. Mentum bilobed, cephalic margin untoothed. Coloration black; breathing tube light yellow.

Pupa.— Right breathing horn very short, degenerate. Fore tarsi overlying middle tarsi. Tubercles on abdomen moderately elongated, not crowned by a circlet of spines as in Bittacomorpha, but tipped with a long seta.

The genus Bittacomorphella contains but two described species, the genotype, *B. jonesi* (Johns.), and the larger *B. sackenii* (Röder) from western America, the immature stages of which are wholly unknown. There is no published literature on the biology of this group of crane-flies.

Bittacomorphella jonesi (Johns.)

1905 *Bittacomorpha jonesi* Johns. Psyche, vol. 12, p. 75–76.

Bittacomorphella jonesi is a curious little phantom crane-fly, not uncommon in cold Canadian woods thruout the Northern States, where it is usually found near running water or springs and often in small, dark ravines or along shaded runs. The adult flies sometimes lurk beneath low, dark bridges and culverts, where they are often associated with species of Dolichopeza and Oropeza. An account of the habits of the adults of this species may be found in an earlier paper by the writer (Alexander, 1916b:545–546).

The larval habitat is very different from that of other local species of the family, which, as a rule, prefer open swamps, swales, or wet meadows. The larvae of this species live in rich organic mud in shaded woods. They were first found on the Bool hillside at Ithaca, New York, beneath decaying beech leaves in wet or damp mud which was mixed with old beechnuts, hulls, acorns, butternuts, broken decayed twigs, and similar débris. The Bool area is a very steep hillside with a general northern exposure, heavily shaded with tall forest trees. In former days it extended far to the eastward and was connected with Slim Jim Woods, near the second bridge in Forest Home. The cut area is now a pasture, but patches of skunk cabbage and cat-tails still persist. On the shaded hillside the skunk cabbage occupies pockets or level areas where the soil is largely calcareous. The forest cover consists of beech, hard maple, basswood, yellow birch, red oak, butternut, elm, a few large alders, a few aspens, and on the surrounding hillside a thick stand of hemlock. The shrubs include *Ribes floridum* L'Her., *Cornus alternifolia* Linn. f., and similar species. The herbage at this season is of the dominant skunk cabbage, young seedlings of *Impatiens biflora* Walt., *Geum rivale* Linn., and *Cardamine Douglassii* (Torr.) Britt. In places there are thick mats of mosses, *Brachythecium rutabulum* (Linn.) B. & S., on the limy soil, and Amblystegium on decaying prostrate limbs.

The curious larvae of Bittacomorphella were here found associated with the following crane-fly larvae and pupae: *Dicranomyia stulta*, *Limnophila adusta*, *L.* (*Dicranophragma*) *fuscovaria*, *Ulomorpha pilosella*, Penthoptera, *Molophilus hirtipennis*, *Erioptera megophthalma*, *Ormosia innocens*, *O. nigripila*, *Tipula collaris*, *T. oropezoides*, *T. cayuga*, and others. In addition numerous other natural associates were found, such as the larvae of a carabid beetle, *Nebria sahlbergi* Fisch., sow bugs, mollusks, and a great variety of other organisms. On July 10, 1914, adults of Bittacomorphella were not uncommon in the same association, at which time they were flying with other crane-flies such as *Dicranoptycha germana*, *Molophilus hirtipennis*, *M. pubipennis*, *Erioptera vespertina*, *E. venusta*, and *Gonomyia blanda*.

The first larvae of Bittacomorphella were found on May 11, and at that time were almost fully grown. They present a very remarkable appearance, being black or very dark in color and covered with numerous long projections. The breathing tube, which is capable of entire retraction within the body, is very short, and is light yellow, in contrast with the remainder of the body. The larvae are, as a rule, very slow and sluggish in their movements, but when disturbed they become more active. Large and small larvae, of two distinct sizes only, were often found in the same situations at the same time. A fully grown larva was placed in rearing on June 11, 1917, and emerged as an adult male on June 24. This provides for a pupal duration of not more than thirteen days, but the pupal stage is undoubtedly much shorter.

Larva.— Total length, 15–17 mm.
Length exclusive of breathing tube, 12.5–14 mm.
Length of breathing tube, 2.4–3 mm.; to base of gills, 1.3–1.8 mm.; beyond gills, 1.1–1.2 mm.
Greatest diameter across body, 1.7–2 mm.

Coloration dark brown to almost black, breathing tube light yellowish; in young individuals and occasional older specimens, coloration more rusty.

Body short, stout, cylindrical but appearing depressed, covered with numerous elongate projections. Breathing tube very short and capable of complete retraction within body (Plate XVI, 25). Body appearing proportionately broader, and tapering more abruptly to breathing tube, than in other species of the family herein discussed, this appearance being due to great length of lateral body projections.

The most notable single feature of larva consisting of the numerous projections from body (Plate XVII, 33), these being incased in a blackened, horny substance which is somewhat brittle. Usual shape of body extensions cylindrical, slender, and generally simple

except for those near end of body, which are asymmetrically once-forked. Basal half of projections heavily chitinized, but distal end almost transparent. Entire surface of projections beset with numerous transverse rows of short hairs, usually about nine to twelve hairs in each row, nine and ten being common, these hairs doubtless serving to hold the blackened, horny covering of the projection. Sensory papillae (Plate XVII, 34) borne at or near apices of projections, each with a long bristle; these papillae narrowed at base, thence enlarged to form a head, on which bristle is inserted; usually one or two bristles to each projection, but occasionally an additional one present, which is much smaller and degenerate. Dorsal body projections occupying transverse rows across segments, those near lateral and caudal parts of body being long and powerful, those on median region being short and degenerate; segments of thorax and abdomen subdivided into false segments, these transverse rows occupying caudal margins of these segments, there being usually from four to six of the weak projections between the powerful lateral ones. In addition to these projections, sparse branched hairs lying in the same transverse rows (Plate XVII, 35). Projections at end of body surrounding base of breathing tube all long and powerful, and, as stated above, some weakly bifurcate. Ventral body projections similar to those of dorsum but relatively smaller.

Abdominal pseudopods feebly chitinized at tips, with very large, slightly curved claws which are but little shorter than the pseudopods themselves (Plate XVII, 32). Breathing tube short and stout, surface before apex transversely wrinkled. Papillae rather numerous, bearing sense hairs scattered over surface of tube, those just back of apex short and spine-like, those farther back long and slender, very like and homologous to the bristles terminating the body projections, as discussed above. Gills two, stout, about one-third length of terminal section of breathing tube. Body projections incrusted with a black, horny substance, as discussed above; on lateral projections, apical setae likewise incased, at least basally, producing a bilobed or even a trilobed appearance; this black corneous incrustation brittle and easily removed, leaving projection and bristles intact.

Head subquadrate, sides nearly parallel, occipital foramen ventral in position (Plate XVI, 26); surface of head covered with numerous small, chitinized points which are longest on posterior angles; anterior ventral angle slightly produced; two setiferous punctures on ventral surface, one on either side just behind anterior angles, the other closer to foramen. Dorsum with setae arranged as shown in Plate XVI, 27; setae simple. Labrum (Plate XVII, 31) with four dorsal setiferous punctures along anterior margin, the median pair closely approximated; another powerful seta occupying each lateral angle on dorsal side; dense brushes of long hairs on either side beneath. Epipharynx (Plate XVII, 31) supported by two powerful chitinized arms connecting across midventral region and then extending laterad and expanding outwardly to form posterior margin of labrum; surface of epipharynx with closely appressed teeth. Labium (Plate XVI, 28) with cephalic margin of mentum almost entire, the broad median part produced cephalad and feebly bilobed; palpi with a dense fringe of long hairs around base and with sensory papillae at tips. Antenna (Plate XVI, 30) short, cylindrical, somewhat globular or barrel-shaped; about four elongate papillae and two or three shorter ones, these papillae terminal in position, the largest one occupying the inner side. Mandible (Plate XVI, 29, 30) with the outer angle a powerful hook bearing smaller teeth on ventral face at about midlength; inner angle flattened, and, besides terminal blade, bearing a comb of about five teeth, the innermost being the longest and

slenderest; a dorsal line of strong setae extending from base of outer hook inward; outer edge of mandible with two strong setae, these protected at their bases by small dorsal ears, or projections, from the mandible; dorsal face of mandible with a powerful hinged prostheca; near base of mandible on dorsal face a curious five-lobed sensory organ. Maxilla (Plate XVI, 29) with the cardo triangular, the ventral or outer face with two closely approximated setiferous punctures; stipes triangular, with three strong setae near palpus; palpus antenniform, cylindrical, rather elongated, and with about six sensory papillae at tip, one being much longer than the others; outer lobe of maxilla with cephalic margin blackened and chitinized, inner angle with a dense brush of long hairs.

Pupa.— Length excluding breathing horn, 9.5 mm.
Width, d.-s., 1.7 mm.
Depth, d.-v., 1.4 mm.

The following description is taken from the cast pupal skin of the only specimen that was reared:

Antennal bases approximated on front between eyes. Clypeus bluntly rounded at apex, transversely wrinkled. Lobes of labium (Plate XVII, 36) broad, rounded apically; maxillary palpi short and stout, broad at base, gradually narrowed to the short tip, which is not recurved. (The structure of the head and the eyes indicates some peculiar characters not possessed by the pupae of related genera, but the cast pupal skin is insufficient for accurate diagnosis.) Two bristles below eye and just above base of palpus, and a longer and more slender seta farther laterad. Sides of head behind antennae appear to be produced laterad into blunt points. Right breathing horn small, degenerate, much curved. (In the single pupal skin available, it cannot be determined whether the left horn has been broken off or is undeveloped.) Just laterad of each breathing horn a small tubercle bearing a long seta. Scutal lobes with about four stout setae. Tarsal sheaths of fore legs, as in the subfamily, overlying the middle pair but shorter (Plate XVII, 37).

Abdomen with chitinized bands extensive, as in Bittacomorpha. Arrangement of tubercles about as in other species of family. Tubercles shorter and weaker than in Bittacomorpha and not crowned by a circlet of spines, each being tipped with one or more (four or five) long setae (Plate XVII, 38); the pleural tubercles the longer and many of them multisetose. Cauda of male, in general features, similar to that in Bittacomorpha, the dorsal median lobe (Plate XVII, 39) stout, the ventral horns (Plate XVII, 40) short and powerful, directed laterad; horns on dorsal lobes apparently lacking.

Nepionotype.— Ithaca, New York, May 30, 1917.
Neanotype.— Cast pupal skin, reared June 23, 1917.
Paratypes.— Topotypic, May 15 to June 10, 1917.

Genus **Bittacomorpha** Westwood (Gr. *Bittacus* + *shape*)

1835 *Bittacomorpha* Westwood. London and Edinburgh Phil. Mag., vol. 6, p. 281.

Larva.— Form elongate, body gradually narrowed behind into the partly retractile breathing tube. Integument with transverse rows of tubercles. Pseudopods on abdominal segments 1 to 3 prominent, with large curved claws. Head subpyriform, dorsum with rows

of prominent black spots converging behind. Mandible stout, with a single powerful outer tooth. Mentum bilobed, anterior margin not comblike. Color of body, rusty red.

Pupa.— Right pronotal breathing horn very elongate; the left very small and short, subdegenerate. Fore tarsi overlying middle tarsi. Tubercles on abdomen very long, located on broad transverse bands of chitin, each tubercle with a star of four or five spines surrounding the apex, which bears a long seta.

The genus Bittacomorpha, as here restricted, includes but two species — the genotype, *B. clavipes* (Fabr.), and *B. occidentalis* Ald. of western America, concerning the biology of which nothing has been recorded. The literature on the immature stages of *Bittacomorpha clavipes* is summarized under the family account (page 773).

Bittacomorpha clavipes (Fabr.)

1781 *Tipula clavipes* Fabr. Spec. Ins., vol. 2, p. 404.
1835 *Bittacomorpha clavipes* Westw. London and Edinburgh Phil. Mag., vol. 6, p. 281.

Bittacomorpha clavipes, the "phantom crane-fly," is a common and widely distributed species thruout North America east of the Rockies. It is easily recognized by the black-and-white-banded legs, with their conspicuously enlarged and swollen metatarsi. The species is very characteristic of alder swamps and the wet margins of ponds. While in copulation the insects often fly, the female ahead, the male trailing on behind like the tail of a kite. When they alight on a plant stem, the female is invariably uppermost, the male often hanging free with none of its feet on a support. The swollen metatarsi are almost completely filled by the tracheae, and these serve to buoy the insects as they drift about in the wind. Brues (1900) describes these peculiar tracheal dilations in detail. He says, in part:

When flying, Bittacomorpha uses the wings scarcely at all, relying in great measure upon wind currents for transportation. The legs are exceedingly light, as the exoskeleton is thin and delicate, and encloses practically no tissue which can serve to increase their weight.

In a letter from Dr. J. G. Needham, dated September 27, 1917, valuable data on this habit of drifting are furnished, as follows:

Yesterday while crossing the Fall Creek bridge near my home on Cornell Heights, I made an observation on Bittacomorpha that interested me greatly. A breeze was blowing up the gorge, and on the breeze a Bittacomorpha was drifting rapidly upward in the usual flight attitude, with broadly outspread legs, the swollen metatarsi hanging vertically, all phantom-like in slenderness and in strongly contrasting black and white. It came up from below the level of the rail, swept past within two feet of my face, and passed on upward with the breeze until lost to view, perhaps 100 feet higher than the bridge, and much farther upstream. Since

the creature can fly only very slowly and here was moving several times faster (I could not see whether it was using its wings), it was obviously drifting in the wind. Perhaps this is a normal function of the expanded metatarsi.

The larvae are usually abundant in decaying vegetable matter in rich organic mud about ponds and in swamps. The writer has found them especially numerous in the Basin Swamp at Orono, Maine (in 1913), and near Round Pond at McLean, New York. At Orono they were associated with larvae and pupae of *Ptychoptera rufocincta*, *Limnophila macrocera*, *Pilaria tenuipes*, *P. recondita*, *Erioptera chlorophylla*, a variety of chironomid larvae, numerous larvae of Trichoptera in their cases, nematodes, and leeches. Needham and Betten (1901:574–575) give a summary of the larval habitat of this species as they found it in the northern Adirondacks. Weston and Turner (1917:53) have recorded the larvae as being scavengers and thus serving as important factors in the elimination of sewage in the Coweeset Stream near Brockton, Massachusetts.

The immature stages of this interesting crane-fly have been well considered by Hart (1898 [1895]:189–195), whose account has been briefly summarized by Howard (1912:95–96). The larvae are found in shallow water that is filled with decaying vegetable matter. Here they live in the mat of dead stems of rushes, grasses, and willow leaves, in semi-stagnant or slowly flowing water. The larvae are elongate-cylindrical, with a long, partly retractile breathing tube. They are deep rusty red or brown in color, quite distinct from the pale whitish larvae of Ptychoptera or the black larvae of Bittacomorphella. They feed on decaying vegetable matter, diatoms, and mud that is filled with organic matter. They rest beneath the surface of the water, with the tip of the extended breathing tube at the surface film or just beneath the surface, in the latter case breathing by means of the small tracheal gills. When about to pupate, the very long, coiled breathing tube of the pupa is wound around the thorax beneath the larval skin. On pupation the tube soon straightens out into a very long, stiff, bristle-like structure. Like the larvae, the pupae rest beneath the surface of the water, with the tip of the breathing tube projecting above the surface film. The pupal duration is apparently about a week.

Larva.— Length when fully extended, about 60 mm.
Length of breathing tube, about 20 mm.
Diameter of body, about 2.6 to 3 mm.

Body tapering gradually at either end, posterior end prolonged into breathing tube. Usual color pale rusty brown, but the writer has found a few nearly full-grown specimens which were as pale in color as the larvae of Ptychoptera. Body covered with numerous transverse rows of small tubercles, or papillae, which bear short setae. Head broadly ovate, convex above, where it is conspicuously marked with rows of black spots, these interrupted lines converging behind. Mouth parts in general similar to those in Bittacomorphella, the main points of difference being as follows: mandible (Plate XVIII, 42) shorter and stouter, ending in a powerful outer tooth, the comb of inner teeth being reduced to about eight small tubercles, the two bristles on outer margin of mandible not overlapped by projecting " ears "; labium (Plate XVIII, 41) shorter and stouter, with a different arrangement of papillae; epipharynx long, narrowed behind, distinctly bilobed, each half with parallel rows of long, comblike teeth projecting proximad; anterior comb of epipharynx with the anterior teeth the largest, the teeth gradually reduced in size behind; posterior comb with the rows of teeth widely separated anteriorly, approximated behind so as to be contiguous or nearly so at their ends; space between these rows filled with long hairs; anterior teeth small and feebly chitinized, posterior teeth stronger. First three abdominal segments bearing conspicuous pseudopods, each terminated by a sharp, slender claw which fits into a groove on the face of the pseudopod.

Pupa.— Total length, 40–60 mm.
Length excluding breathing tube, 15.5–25 mm.
Length of breathing tube, 25–35 mm.
Degenerate breathing tube, length 2 mm., diameter 0.2 mm.
Width, d.-s., 1.8 mm.
Depth, d.-v., 2.6 mm.

Breathing tube light brown; wing sheaths brown; leg sheaths light brownish yellow and dark brownish black, alternated, corresponding to the leg markings of the adult fly. Abdomen pale yellow, rather uniformly covered with abundant brownish tubercles and transverse, chitinized plates, these brown areas scarcer on pleura and not especially abundant on apical margins of segments.

Pupa somewhat similar in general structure to pupa of Ptychoptera. Anterior cephalic crest small, lobules rounded, each tipped with a long, stout seta; immediately behind anterior crest, a similar blunt, bilobed projection of front; laterad of crest, a slender, elongate tubercle on either side, immediately behind antennal sheaths, each with a long seta; two other setiferous tubercles on head behind antennae and maxillary palpi. Antennal bases approximated between eyes. Sides of head, laterad of eyes, with a small setiferous tubercle. Maxillary palpi not recurved at tip, as in Ptychoptera, ending opposite knee joint. Clypeus elongate, gradually narrowed toward apex, transversely wrinkled; two hairs toward base near inner margin of eye. Each half of labium broad, roughly subquadrate, tips broadened and obliquely truncated (Plate XVIII, 43).

Breathing horns almost as in Ptychoptera. (Nearly always it is the right horn that is elongated, but in about ten per cent of the specimens the left horn is elongated while the right is degenerated; Hart records one specimen in which both horns were developed, but unequally, the right measuring 23 mm. and the left 13 mm.; some of the specimens recorded by Hart are larger than any that the writer has ever seen.) Wing sheaths ending almost opposite tips of fore tarsi; media unbranched. Leg sheaths (Plate XVIII, 47) with fore tarsi much shorter

than the others and lying directly over middle tarsi; tarsi of hind and middle legs parallel and extending beyond tips of fore tarsi. Scutal lobes each with about four setiferous tubercles. Thorax and first abdominal segment transversely crenulated.

Abdomen with transverse bands of chitin much broader than in Ptychoptera, so that they cover almost the entire abdominal surface; these bands with about twelve tubercles on segments 3 and 4, about ten on segment 5, and from six to eight on the posterior segments; tubercles of various sizes, small and somewhat degenerate ones being interspersed with larger ones; tubercles long and slender, each crowned by a circlet or star of from three to six (usually four or five) stout spines (Plate XVIII, 44–46), a setiferous papilla arising from the center of this circlet of spines; spines on pleura longer than those on remainder of abdomen, but not arranged in distinct longitudinal rows as in Ptychoptera, being usually more irregular, in some cases showing three or four more or less distinct rows; these pleural chitinized areas usually bearing from two to four tubercles, which are closely approximated basally so as to present a somewhat branched appearance. Male cauda (Plate XVIII, 48) as in Ptychoptera, but dorsal median lobe very short and stout; tubercles on segment immediately before cauda long and slender, similar to those on remainder of abdomen.

Nepionotype.— Ithaca, New York, May 15, 1917.
Neanotype.— Orono, Maine, June 24, 1913.
Paratypes.— With the type pupa.

Malloch's figure of the pupa (1915–17 b: pl. 35, fig. 6) is diagrammatic. It was probably made from a female individual, the antennal sheaths being shorter in this sex than in the male.

FAMILY Rhyphidae

Larva.— Body eucephalous, amphipneustic. Mandibles opposed. Eyespots distinct. Spiracles on sides of prothorax. Thoracic and abdominal segments divided by false constrictions. Spiracular disk surrounded by two or five lobes (Rhyphinae) or by four lobes (Trichocerinae), or unprovided with lobes (Mycetobiinae).

Pupa.—Head with a bilobed setiferous cephalic crest. Palpi stout, straight. Pronotal breathing horns short, not prominent. Tarsal sheaths lying in pairs, one above another, the fore legs lying on the middle legs, and these latter on the hind legs. Lateral abdominal spiracles small but distinct.

The family Rhyphidae includes an apparently heterogeneous group of genera which are in reality very closely related. The adults are of diverse appearance, but the immature stages are exceedingly similar to one another and undoubtedly all three of the groups included in the family are closely allied.

The immature stages of the Rhyphinae (Rhyphus) have been discussed by many entomologists, among others by Johannsen (1910:35–36,

Rhyphus punctatus) and by Malloch (1915–17 b: 243, *R. punctatus*). The larvae are often handsomely banded and mottled with brown or purplish. Johannsen and other authors describe the cauda as ending in two short lobes, but Malloch mentions five such lobes. The general structural characters are those described above for the family. The larvae occur in decaying vegetable matter, in manure (especially horse and cow dung), in sewage, and in similar material.

The Mycetobiinae are represented by Mycetobia, a curious fly which superficially resembles a mycetophilid rather than a crane-fly. Long ago Lyonet, Dufour, Guérin-Méneville and others described and figured the larva of Mycetobia and noted the eucephalous condition of the head and the amphipneustic spiracles. Osten Sacken (1863) first suspected the affinities of this genus with Rhyphus. More recently, work by Johannsen (1910: 31–32), Malloch (1915–17 a, and 1915–17 b: 244–245), Edwards (1916), Knab (1916), and others has definitely settled the relationship of this insect with the Rhyphidae. The larvae and the pupae agree closely with the general family characters discussed above. The larvae occur in decaying wood and about fermenting sap in wounds of trees. The genera Ditomyia Winn. and Symmerus Walk. are now placed in a separate family from Mycetobia, the Ditomyiidae (Keilin, 1919).

Until recently, the Trichocerinae have been considered as being members of the family Tipulidae. They include only the genus Trichocera, with about twenty-five nominal species, and, presumably, Ischnothrix Bigot, represented by a single species from Cape Horn. From the general appearance of the adult, these flies have usually been referred to the tribe Limnophilini, in a position near the genus Limnophila. Brunetti (1912) referred them to the Pediciini, and most other recent workers have accorded them tribal or subfamily rank in the Tipulidae. Bezzi (1914: 214), influenced by the work of Keilin (1912), referred Trichocera to the Rhyphidae, but later (1918 a: 20) placed it back in the Tipulidae (as Limnobiidae). Malloch (1915–17 b: 234) likewise places Trichocera with the Tipulidae, but mentions the close resemblance of the larva to that of Rhyphus. The best discussions of the morphology of the larva and the pupa are those by Keilin (1912) and De Meijere (1916: 191–194), both of whom were strongly impressed by the striking resemblance of the larva to that of Rhyphus. In the present paper, the Trichocerinae is the only group considered in detail.

SUBFAMILY **Trichocerinae**

Genus **Trichocera** Meigen (Gr. *hair* + *horn*)

1800 *Petaurista* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*).
1803 *Trichocera* Meig. Illiger's Mag., vol. 2, p. 262.
1911 *Paracladura* Brun. Rec. Indian Mus., vol. 6, p. 286.

Larva.— Body eucephalous, amphipneustic. Thoracic segments divided into two annuli. Spiracles on lateral margin of posterior ring of prothorax. Abdominal segments divided into three annuli. Cauda ending in four lobes, ventral lobes the longer and more slender; lobes bearing numerous stout hairs near tips on outer face. Eyespots distinct. Lateral plates of head widely separated on midventral line. Mandible with prostheca distinct.

Pupa.— Cephalic crest small, lobes with stout setae. Clypeus short; labrum dumb-bell-shaped; palpal sheaths stout. Antenna elongate. Leg sheaths lying in pairs above one another, gradually lengthening, fore pair the shortest, posterior pair the longest. Pronotal breathing horns short. Abdominal spiracles small, but distinct and functional.

The small winter gnats of the genus Trichocera are rather familiar, since they are not rare during the winter months in cellars or even in the open on warm days, occurring in sunlit places in small, dancing swarms. They are abundant during fall and spring. They occur also in cool, shady places in summer, but are less in evidence at this season.

Trichocera is found somewhat commonly and regularly in mines, often at very considerable depths. Boheman (1850) records specimens of *T. regelationis* in mines 600 feet below the surface, and Lampa (1890) also records the species as being found at considerable depths. Dr. H. B. Hungerford found numerous adults of a species of Trichocera in the Amethyst silver mine near Creede, Colorado, in 1914. Specimens that he obtained were taken at the sixth level, but the miners said the insects were to be seen in all parts of the mine; along the laterals at the sixth level they were noted 7000 feet from the entrance. It is supposed that these individuals breed in the animal waste which naturally accumulates in such places. Trichocera is also a characteristic inhabitant of caverns and grottoes, all stages being found in such situations (Schmitz, 1909:80; Bezzi, 1911–12:46–47, 49, and 1914:214).

The swarming and mating of these flies is well known. It has been ably described by Ainslie (1907), and is here discussed only in general terms. The insects swarm commonly in the autumn. Sometimes the swarms include but comparatively few individuals, but at other times many thousands participate. They swarm usually from five to twenty-five feet above the ground, all facing in the same direction, that is,

toward the wind or breeze. Mating takes place in the air, and united pairs then fly away or drop to the ground beneath. The swarms are often very dense, and individuals come in frequent contact with one another. When the breeze shifts, the swarm immediately readjusts its position and direction.

The immature stages of Trichocera are spent in decaying vegetable matter, beneath dead or decaying leaves, in débris, in fungi, and in similar situations. Sometimes the larvae and pupae are rather numerous in stored roots and tubers, especially potatoes, in which cases they may assume an economic importance (Johannsen, 1910:34–35; Carpenter, 1912). The specimens used by the writer for study are part of Johannsen's material, determined as *T. regelationis* from Patten, Maine. The taxonomic condition of the group is such that no specific identification of the adult flies can be attempted at this time. The immature stages of the generalized subgenus of Trichocera, Diazosma Bergroth, are unknown.

The most important literature on the genus Trichocera is as follows:

Trichocera regelationis	General	Dufour, 1840:161.
Trichocera regelationis	Larva, general	Schmitz, 1909:80, pl. 8, fig. 3.
Trichocera regelationis	Larva, pupa	Johannsen, 1910:34–35, figs. 51–57.
Trichocera regelationis	Pupa	De Meijere, 1916:194.
Trichocera hiemalis	Larva, general	Curtis, 1846b.
Trichocera hiemalis	General	Cameron, 1917:63.
Trichocera fuscata	General	Carpenter, 1912. (Damage.)
Trichocera sp	Larva	Bremi-Wolf, 1846:175.
Trichocera sp	Larva	Perris, 1847:37, pl. 1, fig. 3.
Trichocera sp	General	Bezzi, 1911–12:46–47, 49.
Trichocera sp	Larva	De Meijere, 1916:191–194, figs. 21–23.
Trichocera sp	Larva, pupa	Keilin, 1912. (Morphology.)
Trichocera sp	Larva	Malloch, 1915–17b:234–235, pl. 26, fig. 1; 306.

Trichocera regelationis, supposition.

Larva.— Length, 8–9.5 mm.
Diameter, 1 mm.

Coloration pale brown in preserved material, whitish in fresh specimens.

Body rather short, cylindrical to slightly depressed (Plate XIX, 49). Pseudopods lacking. Head complete, non-retractile, strongly chitinized; lateral plates of head widely separated on midventral line, connected only by a narrow bridge posteriorly; chaetotaxy as shown (Plate XIX, 52 and 53). Mandibles opposed, of three parts, principal segments bearing on inner side near base an apparently movable appendage (prostheca) which has, besides the large apical tooth, three smaller teeth. Labrum bluntly rounded, with long hairs. Epipharynx with lateral combs of about six blunt teeth. Antenna two-segmented; basal segment

very short, disk-shaped, inserted on a large brown-margined plate which is part of the head chitin; second segment much narrower, egg-shaped; in addition to this segment there are several small sensory papillae on the end of the first segment.

Segments of body divided into secondary annuli, thoracic segments with two such rings, abdominal segments with three; annuli bearing transverse rows of short setae. Anterior spiracles on posterior ring of prothorax near lateral margin conspicuous, smaller than posterior spiracles but constructed on same general principle. Spiracular disk surrounded by four lobes; ventral lobes longer and more slender than dorsal pair, inner face narrowly chitinized, outer face densely clothed with abundant short yellow hairs (Plate XIX, 50 and 51); dorsal lobes shorter and blunter, with short hairs on apices of outer face. Spiracles large, at base of dorsal lobes.

Pupa.— Length, 7.5–7.8 mm.
Width, d.-s., 1.4 mm.
Depth, d.-v., 1.4 mm.

Coloration whitish; head, thorax, and sheaths of appendages brown.

Anterior cephalic crest small, lobes widely separated, each tipped with a long, stout seta directed ventrad; a tiny seta just behind each anterior lobe. Antennal bases above and slightly between the eyes, bent dorsad and thence caudad, passing behind joints of legs, in the female attaining to about one-third length of wing. Frontal region between eyes slightly tumid, somewhat shiny. Clypeus short, the sides parallel, the apex U-shaped; labrum broad, dumb-bell-shaped, the caudal margin concave. Maxillary palpi very short and stout, ending before knee joints of fore legs (Plate XIX, 55). A small tubercle just laterad of base of antenna. Each cheek produced into a long, blunt, wrinkled tubercle.

Mesonotum (Plate XIX, 54) strongly gibbous, pale medially, narrowed in front, anterior margin truncated and sending a sharp median carina cephalad; sides of mesonotum opposite wing root with four small setae, in two slightly separated groups. Anterior angles of pronotum with a short bristle. Breathing horns small, short and almost straight, broad basally, apical half narrow, inner face fused or closely approximated with pronotum, apex cleft. Wing sheaths attaining level of tips of fore tarsi; venation rather distinct. Leg sheaths with fore legs stout; fore tarsi overlying middle tarsi (Plate XIX, 55); middle tarsi overlying hind tarsi; terminal segments of tarsi swollen. Abdominal segments divided into about three false annuli; caudal margin of each segment fringed with short hairs. Tiny abdominal spiracles on pleural segments. Female ovipositor (Plate XIX, 56) with the dorsal valves short, widely separated, acutely pointed; ventral acidotheca elongate, approximated, bent slightly ventrad.

Larvae and pupae.— Patten, Aroostook County, Maine, May 3 and 23, 1907.

FAMILY Tipulidae

The family Tipulidae is the largest group of crane-flies, and possibly the only one to which the name is justly applicable. It includes a vast number of species (nearly three thousand), arranged in about one hundred

and forty genera. The species are found in most parts of the world, being restricted only by intense heat and cold. Crane-flies require moisture in order to complete their development, and, as a consequence, are almost always found in the neighborhood of flowing or stagnant water. No species known to the writer are inhabitants of desert conditions, the nearest approach probably being some Eriopterini, such as Helobia, Trimicra, and other genera.

The immature stages frequent very wide ranges of habitat, which are indicated elsewhere (page 716). They are readily separable from other related species by the characters outlined on pages 744 to 758. The subfamilies of Tipulidae may be separated by the following keys:

Larvae

1. Body provided with elongate spines or leaflike projections. **Cylindrotominae,** *pars* (p. 959)
   Body without distinct spines..2
2. Form depressed, with more or less distinct lateral tubercles; terrestrial on spermatophytic plants..**Cylindrotominae,** *pars* (p. 959)
   Form terete; if depressed, without tubercles..3
3. Spiracular disk surrounded by six or eight lobes..................**Tipulinae** (p. 974)
   Spiracular disk not as above..4
4. Spiracular disk surrounded by two, four, or five lobes..5
   Spiracular disk with three lobes or without distinct lobes..7
5. Head capsule massive, the hypopharynx a flattened plate with few teeth; size large (aberrant Tipulinae)..6
   Head capsule massive or dissected, if the former the hypopharynx not as above; size usually small..**Limnobiinae,** *pars* (p. 793)
6. Spiracular disk with five lobes; lives in moss..........Genus *Dolichopeza* Curt. (p. 981)
   Spiracular disk with four slender, hornlike lobes; lives in earth. *Tipula selene* Meig. (p. 1016)
7. Size large (30 mm. or over); form very stout, terete; head capsule of the tipuline type; lives in wood..............................Genus *Tanyptera* Latr. (p. 988)
   Size small (20 mm. or under); form slender, terete; head capsule of the limnobiine type. **Limnobiinae,** *pars*. (p. 793)

Pupae

1. Basal abdominal segments unarmed with teeth or spinous projections before posterior margin..2
   Basal abdominal segments armed with a transverse row of usually small teeth or chitinous projections before posterior margin..3
2. Last larval skin adhering to posterior end, attaching pupa to a plant stem or a leaf; coloration bright green..........................**Cylindrotominae,** *pars*.(p. 959)
   Not as above..**Limnobiinae,** *pars* (p. 793)
3. Maxillary palpi curved or recurved at tips; size large, usually 12 mm. or over. **Tipulinae,** *pars* (p. 974)
   Maxillary palpi not recurved at tips..4
4. Maxillary palpi long, slightly or decidedly curved at tips; size large, length usually 12 mm. or over..5
   Maxillary palpi short, straight; size small, usually 10 mm. or under. **Limnobiinae,** *pars* (p. 793)

5. Dorsal abdominal segments with two slender spines before margin.
Cylindrotominae, *pars* (p. 959)
Dorsal abdominal segments with four or more teeth or spines before margin.
Tipulinae, *pars* (p. 974)

SUBFAMILY Limnobiinae

The subfamily Limnobiinae includes a vast assemblage of usually small crane-flies. Only a few genera approach the ordinary size of the other principal subfamily, the Tipulinae, such genera being Limnobia, Psaronius, Limnophila, Eriocera, Pedicia, and a few others.

The writer has endeavored to key the immature stages of tribes, subtribes, and genera. As has been stated elsewhere, the keys are based almost entirely on material seen by the writer, and additional specimens of other species will undoubtedly modify the arrangement very considerably. It is believed, however, that the keys as given will at least furnish suggestions or a basis for succeeding work. The characters given in the keys, in so far as is possible, are those that can be seen without making a detailed dissection of the specimen. However, for most species it is necessary to study the larval head, as already outlined (page 741). The character of "head massive" or "head rodlike" can often be detected thru the larval integument without dissection. The spiracular disk is usually studied without especial difficulty.

The immature stages of the majority of the species are spent in moist earth, usually near water. Some are nearly, if not quite, aquatic (Antocha, Elliptera, some Dicranomyia); others are fungicolous (Ula, some Limnobia); several live under the bark of trees (some Dicranomyia, some Rhipidia, Discobola, Gnophomyia, Teucholabis, Elephantomyia, and others); one, at least, mines in the leaves of plants (Dicranomyia).

The habits of the various genera and species are discussed in greater detail under the respective titles. The following keys separate the tribes and the subtribes of the subfamily Limnobiinae:

Larvae

1. Spiracular disk provided with two long ventral lobes........2
   Spiracular disk not as above........3
2. Spiracles lacking or vestigial; mentum not completely divided medially; hypopharynx a chitinized double comb; species aquatic, in silken cases.
   Limnobiini, subtribe *Antocharia* (p. 799)
   Spiracles large, prominent, exposed; mentum completely divided medially; hypopharynx labriform........*Pediciini* (p. 894)
3. Spiracular disk surrounded by four or five lobes........4
   Spiracular disk surrounded by three lobes or without distinct lobes........19

4. Head capsule massive, compact, the posterior incisions usually shallow..........5
   Head capsule of four or six slender rods, the posterior incisions profound..........15
5. Mentum completely divided, a toothed plate on either side; abdominal segments without distinct creeping-welts..........6
   Mentum, if present and chitinized, not completely divided; abdominal segments with basal creeping-welts..........8
6. Spiracular disk squarely truncated, surrounded by five lobes........*Eriopterini* (p. 908)
   Spiracular disk with four lobes..........7
7. Each mental plate four-toothed; hypopharynx labriform. *Pediciini*, subtribe *Adelphomyaria* (p. 895)
   Each mental plate with seven or eight teeth; hypopharynx a comblike ring. *Hexatomini*, subtribe *Pseudolimnophilaria* (p. 848)
8. Spiracular disk with five lobes..........9
   Spiracular disk with four lobes..........12
9. Antennae almost globular, with two conical apical papillae; lives in fungi. *Hexatomini*, subtribe *Ularia* (p. 838)
   Antennae elongate-cylindrical..........10
10. Abdomen with dorsal and ventral creeping-welts; mentum with more than five teeth. *Limnobiini* (p. 795)
    Abdomen with six ventral welts only; mentum with five or fewer teeth..........11
11. Mentum five-toothed; lives in earth........*Limnobiini*, subtribe *Rhamphidaria* (p. 830)
    Mentum three-toothed; lives in wood.....*Hexatomini*, subtribe *Epiphragmaria* (p. 843)
12. Antennae almost globular, with two conical apical papillae; lives in fungi. *Hexatomini*, subtribe *Ularia* (p. 838)
    Antennae elongate-cylindrical..........13
13. Abdomen with dorsal and ventral creeping-welts, the latter naked; mentum not three-toothed; forms aquatic..........*Limnobiini*, subtribe *Ellipteraria* (p. 806)
    Abdomen with ventral creeping-welts only; mentum with only three primary teeth; species not aquatic..........14
14. Form long, slender; skin naked, shiny, transparent; apical segment of antennae elongate, as long as, or longer than, basal segment; mentum with a smaller tooth on either side; lives in earth..........*Limnobiini*, subtribe *Dicranoptycharia* (p. 828)
    Form short, stout; skin white, opaque; apical segment of antennae short, hemispherical; mentum without small lateral teeth; lives under bark. *Hexatomini*, subtribe *Epiphragmaria* (p. 843)
15. Blades of maxillae not produced; form long and slender..........16
    Blades of maxillae produced into flattened elongate appendages, the tips of which protrude from the thoracic orifice when the head is completely retracted; form short and stout..........17
16. Spiracular disk squarely truncated, surrounded by five lobes which are fringed with numerous, usually short, hairs; esophageal region not conspicuously grooved. *Eriopterini*, subtribe *Eriopteraria* (p. 911)
    Spiracular disk surrounded by four lobes, each ventral lobe with a single elongate bristle; esophageal region elongate, grooved; lives under bark. *Eriopterini*, subtribe *Elephantomyaria* (p. 952)
17. Mental region a narrow, transverse, chitinized bar. *Hexatomini*, group *Limnophilae* (p. 858)
    Mental region not chitinized..........18
18. Mandibles hinged; maxillae and labrum densely hairy; dorsal plates of head capsule united into a spatula..........*Hexatomini*, group *Ulomorphae* (p. 869)
    Mandibles not hinged; maxillae and labrum not densely hairy; dorsal plates of head capsule separated..........*Hexatomini*, subtribe *Hexatomaria* (p. 876)
19. Head capsule massive, compact..........20
    Head capsule of six slender rods; lives under bark. *Eriopterini*, subtribe *Eriopteraria* (p 911)

20. Mental plates not completely divided; abdominal segments with basal creeping-welts on both ventral and dorsal surface; spiracular disk indistinctly four- or five-lobed. *Limnobiini* (p. 795)
Mental plates completely divided; abdominal segments without welts; spiracular disk obliquely truncated. . . . . *Eriopterini* (p. 908)

Pupae

1. Pronotal breathing horns eight-branched; forms entirely aquatic. *Limnobiini*, subtribe *Antocharia* (p. 799)
Pronotal breathing horns simple, unbranched. 2
2. Rostral sheath elongated; lives in wood. . *Eriopterini*, subtribe *Elephantomyaria* (p. 952)
Rostral sheath not elongated. 3
3. Pronotal breathing horns very minute, conical, visible only with a lens.[5] *Limnobiini*, subtribe *Dicranoptycharia* (p. 828)
Pronotal breathing horns larger, not microscopic. 4
4. Dorsal spiracles on eighth abdominal segment large and functional. 5
Dorsal spiracles on eighth abdominal segment small or lacking. 7
5. A large circular spinous area on abdominal pleurites; cephalic crest chitinized, acutely pointed; pronotal breathing horns directed ventrad; lives in decaying wood. *Hexatomini*, subtribe *Epiphragmaria* (p. 843)
Not as above. 6
6. Pronotal breathing horns large, flattened, the tips yellow; abdominal tergites with shagreened crossbands. . . . . *Hexatomini*, subtribe *Ularia* (p. 838)
Pronotal breathing horns slender, cylindrical; abdominal tergites with tranverse rows of small spines. . . . . *Limnobiini*, subtribe *Rhamphidaria* (p. 830)
7. Abdominal pleurites with circular areas set with numerous microscopic spicules; pronotal breathing horns short, usually truncated at tips, which are margined with the breathing pores. . . . . *Pediciini* (p. 894)
Abdominal pleurites not as above, if with spines these large and few in number; pronotal breathing horns long, cylindrical. 8
8. Abdominal segments with broad transverse bands or welts on basal rings of third to seventh tergites. . . . . *Limnobiini* (p. 795)
Abdominal segments with basal ring unarmed as above, posterior ring before margin with a transverse row of spines or stiff setae. 9
9. A distinct crest on mesonotal prescutum armed with tubercles, spines, or setae; size small (usually under 9 mm.). . . . . *Eriopterini* (p. 908)
No distinct crest on mesonotal prescutum (scutellum armed in some Eriocera); size large (usually over 10 mm.). 10
10. Leg sheaths very short, barely exceeding wings; lives under bark. *Eriopterini*, genus *Gnophomyia* (p. 934)
Leg sheaths longer, extending one or more segments beyond tips of wings. 11
11. Size small (under 6 mm.); abdominal armature weak, lacking on segment 7. *Pediciini*, subtribe *Adelphomyaria* (p. 895)
Size larger; abdominal armature stronger, spinous; if small in size (Dicranophragma), basal annuli of abdominal segments armed with naked tubercles. . *Hexatomini* (p. 835)

Tribe **Limnobiini**

A large group of crane-flies, arranged in a few often extensive genera, comprise the tribe Limnobiini. At first sight the tribe appears to be a

[5] In the genus Cladura (Eriopterini), reared while this paper was going thru the press, the breathing pores are likewise microscopic, being entirely sessile (page 949).

heterogeneous assemblage, but in reality it constitutes a natural group. The tribe as herein arranged includes the old group Limnobiini, with the addition of several genera that were formerly distributed in the Antochini. The divisions of the tribe as now constituted are as follows:

1. Limnobaria — including the old tribe Limnobiini.
2. Ellipteraria — including the genus Elliptera. This is close to the preceding subtribe and may be a group belonging to it.
3. Antocharia — including Antocha and presumably allied genera, as Orimargula, Orimarga, Diotrepha, and possibly others.
4. Rhamphidaria — including Rhamphidia and its allies.
5. Dicranoptycharia — including Dicranoptycha only.

These groups are not far removed, phylogenetically, from the lowermost divisions of the Hexatomini, such as the Ularia and the Epiphragmaria, and the two tribes are unquestionably closer together than their arrangement on paper would indicate. The separation of the two major groups was made largely on the characters of the imagines.

The larvae have the body terete, moderately elongate or very long and slender (Dicranoptycha). The abdominal segments are subdivided into a basal and a posterior ring, the former with transverse welts of microscopic chitinized points or hooks. In the Limnobaria and the Antocharia these welts occur on both the dorsal and ventral surfaces in the form of microscopic hooks; in the Ellipteraria they are on segments 3 to 9 on the dorsal surface only, being indicated on the ventral surface but naked; in the Rhamphidaria the welts are ventral in position on segments 2 to 7; in the Dicranoptycharia they are similar, on segments 2 to 8. The body in Dicranoptycha is entirely glabrous.

The head capsule is of moderate to large size and is massive and compact, consisting of a narrow dorsal plate which is usually indented behind, and two broad mussel-shaped lateral plates which are connected anteriorly across the venter to form the mental plate. The mental plate consists of an outer plate which usually terminates in a single median point, and behind this an inner plate which contributes additional teeth to the mentum. In Dicranoptycha there is but one subequal tooth on either side, with an additional much-reduced tooth; in Rhamphidia there are two teeth, and in the other groups there are usually four or five. The hypopharynx is usually a double plate united at the ends to form a collar, with the anterior margins finely toothed. The maxillae are

large and simple in structure; the cardo and stipes are large; the palpus is flattened. The antennae have the apical segment or papilla ranging from elongate, in Dicranoptycha, to very flattened and disklike, in Limnobia and its allies. The mandibles are usually of simple structure, with one or two dorsal teeth and from three to seven teeth in the ventral cutting row.

The spiracles are lacking in some species, at least, of Antocha. The spiracular disk is surrounded in Rhamphidia by five subequal lobes, in Dicranoptycha by four slender, naked lobes; in many Limnobaria the lobes are lacking or indistinct.

The larvae of many of the species are able to spin silken cocoons or tubes in which they live. These tubes are open at both ends, and are usually covered exteriorly with particles of extraneous matter gathered in the larval haunts.

The pupae usually lack a distinct setiferous cephalic crest, altho one is present in Rhamphidia and in Dicranoptycha. The pronotal breathing horns are usually large, and are either subcircular, or wider than long (most Limnobaria), rarely elongate (Rhamphidaria), very large, earlike, and contiguous or practically so on the median line (Ellipteraria), or branched into eight long filaments (Antocharia); in the Dicranoptycharia, however, they are microscopic. The abdominal segments on the basal ring often show a transverse welt of small hairs or a double convergent row of chitinized hooks; in Discobola, Rhamphidia, and Dicranoptycha, however, this is apparently not the case, the abdominal armature being more eriopterine or hexatomine in appearance. The eighth abdominal segment often bears a pair of dorsal spiracles; these are apparently lacking in some species (*Antocha saxicola*) and are small in most Limnobaria, but are large and functional in Rhamphidia.

The following keys separate the subtribes of the tribe Limnobiini:

Larvae

1. Body ending in two long ventral lobes; spiracles lacking or very reduced; forms strictly aquatic . . . . *Antocharia* (p. 799)
   Body not as above; spiracles large 2
2. Body with ventral and dorsal welts on abdominal segments 3
   Body with ventral welts only 4
3. Spiracular disk surrounded by four lobes which are provided with long fringes of hair; dorsal welts microscopically spiculose; ventral welts naked; species aquatic. *Ellipteraria* (p. 806)
   Spiracular disk not as above; dorsal and ventral welts alike . . . . *Limnobaria* (p. 808)

4. Body moderately elongated, covered with a long, dark pubescence; abdomen squarely truncated at end, surrounded by five lobes, presenting an eriopterine appearance; mentum conspicuously five-toothed........................*Rhamphidaria* (p. 830)
   Body very long and slender, glabrous; abdomen surrounded by four narrow, glabrous lobes; mentum indistinctly five-toothed...................*Dicranoptycharia* (p. 828)

Pupae

1. Pronotal breathing horns branched; forms entirely aquatic..........*Antocharia* (p. 799)
   Pronotal breathing horns simple..2
2. Pronotal breathing horns very tiny, microscopic, conical.......*Dicranoptycharia* (p. 828)
   Pronotal breathing horns large, conspicuous...................................3
3. Pronotal breathing horns large, earlike, contiguous basally; forms aquatic, in silken cocoons..*Ellipteraria* (p. 806)
   Pronotal breathing horns not contiguous basally..............................4
4. Cephalic crest small or lacking; pronotal breathing horns short and broad, rarely elongated; a pair of small spiracles on dorsum of eighth abdominal segment...*Limnobaria* (p. 808)
   Cephalic crest large, setiferous; pronotal breathing horns long and slender, cylindrical; a pair of large spiracles on dorsum of eighth abdominal segment. *Rhamphidaria* (p. 830)

The most important literature on the tribe Limnobiini is as follows:

Antocha saxicola	General	Needham, 1908a: 205.
Antocha sp	Larva	Malloch, 1915–17b: 236–237.
Elliptera omissa	Larva, pupa, general	Mik, 1886b.
Elliptera omissa	Larva, pupa	Grünberg, 1910: 31–32. (Copy.)
Elliptera omissa	Larva, pupa	Malloch, 1915–17b: 226–227.
Thaumastoptera calceata	Larva, pupa, general	Lenz, 1920a.
Limnobia quadrimaculata	General	Von Röser, 1834 (as *annulus*).
Limnobia quadrimaculata	Larva, pupa	Beling, 1873b: 590–591 (as *annulus*).
Limnobia bifasciata	Larva, pupa, general	Bremi-Wolf, 1846 (as *xanthoptera*).
Limnobia bifasciata	Larva, pupa, general	Pastejrík, 1909 (as *xanthoptera*).
Limnobia bifasciata	Larva, pupa	De Meijere, 1916: 198–201.
Limnobia decemmaculata	General	Loew, 1873: 41.
Limnobia decemmaculata	General	Verrall, 1912.
Limnobia flavipes	Larva	Beling, 1886: 202.
Limnobia inusta	General	Beling, 1886: 202 (as *macrostigma*).
Limnobia sexpunctata	Larva	Beling, 1879: 54–55 (as *nigropunctata*).
Limnobia nubeculosa	General	Beling, 1879: 56.
Limnobia obscuricornis	Larva, pupa	Beling, 1879: 55–56.
Limnobia tripunctata	Larva, pupa	Beling, 1873b: 591–592.
Limnobia triocellata	Larva, pupa, general	Johnson, 1906: 2.
Limnobia triocellata	Larva, pupa	Malloch, 1915–17b: 215–216.
Limnobia immatura	Pupa	Malloch, 1915–17b: 216.
Libnotes perkinsi	General	Perkins, 1913: clxxxii (as Limnobia).
Discobola caesarea	Pupa	Mik, 1884.
Dicranomyia trinotata	Larva, pupa	Thienemann, 1909.
Dicranomyia trinotata	Larva, pupa	Grünberg, 1910: 29. (Copy.)
Dicranomyia dumetorum	General	Winnertz, 1853.

Dicranomyia dumetorum	General	Beling, 1873 b: 592.
Dicranomyia dumetorum	General	Beling, 1879: 56.
Dicranomyia dumetorum	Larva	Beling, 1886: 201–202.
Dicranomyia sp.	General	Schubart, 1854.
Dicranomyia foliocuniculator	General	Swezey, 1913.
Dicranomyia foliocuniculator	Larva, pupa	Swezey, 1915: 87.
Dicranomyia umbrata	Larva	De Meijere, 1916: 197–198.
Dicranomyia simulans	Larva, pupa, general	Needham, 1908 a: 214–217.
Dicranomyia simulans	Larva, pupa	Malloch, 1915–17 b: 213–214.
Rhipidia maculata	Pupa	Beling, 1873 b: 592.
Rhipidia maculata	Larva, general	Beling, 1879: 52–53.
Rhipidia uniseriata	Larva, general	Beling, 1879: 53–54.
Rhipidia domestica	General	Johnson, 1910: 704.
Dicranoptycha winnemana	Larva, pupa	Alexander, 1919 b.
Rhamphidia longirostris	General	Gercke, 1884.
Rhamphidia longirostris	General	Grünberg, 1910: 30. (Copy.)
Rhamphidia flavipes	Larva	Hart, 1898 [1895]: 197–199.
Rhamphidia flavipes	Larva	Malloch, 1915–17 b: 231–232.

Subtribe **Antocharia**

The subtribe Antocharia includes the genus Antocha and probably three or four related genera, such as Diotrepha, Orimarga, and Orimargula. The group is well-defined in all stages, so far as these are known, the larvae presenting a curious superficial resemblance to those of Pedicaria, while the pupae introduce a novelty of structure of the breathing horns, which is discussed in detail elsewhere (page 805). It is probable, however, that these peculiarities of larval and pupal structure are largely the result of habit and habitat, and a critical survey of the structure shows a close relationship with the other subtribes herein recognized.

Genus **Antocha** Osten Sacken (Gr. *close approximation*)

1859 *Antocha* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

Larva.— Body slender, tapering behind, ending caudally in two elongate ventral lobes which bear a few hairs at their tips and at intervals along their length. Abdominal segments 2 to 7 each with a swollen area on basal ring densely covered with microscopic hairs. Tracheal gills four in number, large, constricted into three or four lobes. Spiracles lacking or rudimentary. Head capsule moderate in size. Mentum with nine or ten teeth, deeply split behind. Maxilla conspicuous, consisting of two subequal lobes which are provided with dense brushes of hairs. Hypopharynx with chitinized teeth.

Pupa.— Anterior end of body large, tapering behind. Head with a small median lobe in front, on either side of which is a small tubercle; genae gibbous. Pronotal breathing horns large, flattened, the margin branching into eight long filaments. Abdominal segments on basal ring with a double transverse row of small hooks which converge at the ends to inclose an oval depressed area; last segment of body terminating in two strong, recurved, chitinized hooks.

Antocha is a small genus of crane-flies (about seven species) whose specific limits are still not well understood. The species are well distributed thruout the Northern Hemisphere. The adult flies are of primitive organization, but the larvae and the pupae are highly specialized in many respects.

The only previous record of the immature stages of any member of this group is the unknown Limnobiine No. 2 (Malloch, 1915–17b: 236–237), which surely refers to an Antocha, possibly *A. monticola* Alex. The main point of difference between the species described by Malloch and the species described in detail hereinafter is the small spiracles mentioned in the description of the former species. *A. saxicola* lacks spiracles, since it has no use for them, being confined to submerged cases often many feet below the surface of the water.

Altho nothing is known concerning the immature stages of the genera Orimargula, Orimarga, and Diotrepha, the writer believes that these genera will be found to have larvae of this same general type, since from the structure of the adults they are obviously derived from the Antocha stem. The larvae are curiously suggestive of the Pediciini (as compared with Dicranota), but the structure of the mouth parts, the smooth pseudopods, and the cauda, are quite different and indicate that the similarities are analogous only. The pupae are unlike those of any crane-fly as yet made known, in the very remarkable breathing horns; but this is possibly a condition brought about by the habitat rather than a fundamental feature. The apparently very different pupae of Elliptera are closely related to Antocha.

Antocha saxicola O. S.

1859 *Antocha saxicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 219.

Antocha saxicola has one of the most interesting life histories of any of the crane-flies yet discovered, not only because of the larval and pupal habitat, but also because of the peculiar structures that appear in the larva and in the pupa and have been found nowhere else in the immature stages of the family, so far as is known. The larvae simulate strikingly the same stage in the Pedicaria, but are apneustic, entirely lacking functional spiracles and depending wholly on tracheal gills for their respiration. The pupae have the pronotal breathing horns split into eight long filaments, so that they bear a curious superficial resemblance to the pupae

of the black fly (Simuliidae). Both larvae and pupae spend their entire lives in cases on stones in water — usually in running, well-aërated water, and often in the most rushing torrents.

The larvae, as already stated, lack spiracles, the entire respiration being carried on thru tracheal gills, four in number, and the rich tracheal development in the elongate caudal lobes. Thus the tracheal system is truly closed, and represents the maximum of specialization in the reduction in size and final loss of the spiracles. In air-breathing, terrestrial forms, the spiracles are large and situated comparatively close together, gradually becoming smaller and more removed from one another as the creature becomes more and more dependent on blood gills or tracheal gills for respiration. This is the only truly closed tracheal system known to the writer to occur in the Tipulidae. It should be noted that the loss of the spiracles is accompanied by great enlargement of the gills and the taking on of the gill function by the two caudal lobes. The haunt of the larvae is in silken cases on rocks, often in the swiftest part of the stream, where it is impossible to breathe thru spiracles and where the associated forms of life (Ephemerida, Plecoptera, Trichoptera, and Diptera) all, or practically all, depend entirely on gills for respiration.

As a rule, the larval cases are made on rubble or rounded stones, a crevice or a groove caused by inequalities of the rock surface covered over being the simplest and commonest place chosen. The inequalities in the rock are bridged over by a silken, mud- or silt-covered case, which is very delicate and laterally fimbriated with the young larva but becomes much firmer, thicker, and more compact with the older larva and pupa. The larval case is open at both ends and the larva passes backward and forward freely, showing considerable agility when disturbed. When the larva is still small, the case is correspondingly small and insignificant; but the case of the matured larva is conspicuous, measuring from 4 to 5 centimeters in length and about 1.2 centimeters across the lateral "wings," or fimbriations. The insect moves freely along the tube but is very loath to leave it unless actually ejected. As stated above, the late larval and pupal covering is very different from the flimsy, silt-covered tube of the young larva, being smooth, compact, hard, and often covered with pebbles. The pupa has two powerful hooks at its caudal end, enabling it to fasten to the case. In most cases the pupa hangs with the current, head downstream, like the pupa of Blepharocera

and unlike the somewhat similar-appearing pupa of the Simuliidae, which rests with the head upstream, against the current, the pupal case being open at the cephalic end only.

These curious larvae were first noted at Ithaca, New York, in mid-April, in Cascadilla Creek. They were common in situations such as described above. Larvae were found thruout most of April, May, and June; they would probably be seen in somewhat fewer numbers thru most of the summer season, since the adult flies have a long seasonal appearance. The first pupa was found on May 15, 1917, but the season that year was very backward and undoubtedly the species pupates earlier in more nearly normal seasons.

In Cascadilla and Fall Creeks, at Ithaca, the immature stages of Antocha are usually associated with a fauna of rapid-water (lotic) forms, the following being the more notable and constant:

Planarians.	*Planaria* sp.
Ephemeridae.	Nymphs of Baetis, Leptophlebia, Ephemerella, Ecdyurus, Epeorus, Iron, Heptagenia, Chirotenetes, and others.
Perlidae.	Nymphs of Pteronarcys, *Perla immarginata* Say, Acroneuria, Neoperla, and others.
Trichoptera.	Larvae and pupae of Helicopsyche (abundant), Hydropsyche, Hydropsychodes, Ithytrichia, Rhyacophila, Leptocerus, Polycentropus, and others.
Lepidoptera.	Larvae and pupae of Elophila.
Coleoptera.	Larvae of Psephenus.
Diptera.	Larvae and pupae of Blepharocera, Simulium, Orthocladius, Tanytarsus, and others.

Early in spring the rocks are plastered with dense coatings of Diatomaceae (Navicula, Synedra, Meridion, and other genera), which later in the season become much rarer or disappear entirely. It is often impossible to tell the case of Antocha from that of some very similar caddis-worm cases, especially some of the glossosomatine Rhyacophilidae. Dr. Noyes found larvae of Antocha in a small, rapid-flowing stream near Ringwood Hollow, and here the cases were covered with tiny pebbles and it was quite impossible to distinguish them superficially from associated caddis-worm cases. In Cascadilla Creek the little cases of Helicopsyche often plaster the upper surfaces of submerged rocks, and the writer has found tubes of Antocha that were almost buried beneath these cases.

Antocha is by no means confined to rapidly flowing streams, altho the insects are very often found in such situations. The writer has found adults in his tent traps set over the Sacandaga River, in Fulton County, New York, where the water was very quiet and at least ten feet deep. Needham (1908 a: 169–170, 205), similarly, found adults in numbers in his tent traps set over Beaver Meadow Brook at Old Forge, New York, in August, 1905, but did not locate the larvae. In rapid-flowing streams the insects sometimes occur just at the surface in a few millimeters of water, or at greater depths. The immature stages seem adapted to live under almost any conditions of current, from moderate pressure to situations where the water rushes by in torrents and where but few of the usual lotic organisms, such as Blepharocera, Simulium, Psephenus, and others, can exist. From Clemens' studies (1917: 14–23) it is evident that the current is much more rapid just beneath the surface than at various lower depths, so that at a depth of one foot the current velocity is only about two-thirds of that at the surface. Thus these aquatic organisms are not constantly and entirely subjected to such tremendous pressures as on first sight they appear to be. Many of the larvae and pupae perish from desiccation, due to the lowering of the stream level and the consequent exposure of the rocks on which their homes are made.

Copulation between the adult flies takes place on the exposed rocks in and along the margins of the streams where the larvae live (Osten Sacken, 1869: 127). The eggs are deposited in the water, and the entire life, until the emergence of the adult fly, is spent beneath the water. The whole life cycle may require a year, altho the species is possibly double-brooded. At a single time, and even on a single rock, larvae of various sizes, from very small ones to those almost fully grown, may be found, and this probably explains the long flight-period of the adult. That the species is double-brooded remains to be proved.

The food of the larva consists of microscopic plant organisms in the water, the curious maxillae, with their dense brushes of long hairs, undoubtedly being an adaptation for this type of food.

Larva.— Total length, 9.5–10.5 mm.
Length of caudal lobes alone, 1.1–1.2 mm.
Diameter of body, 1–1.1 mm.

Coloration of living larva, light greenish brown above, clearer greenish ventrally; contents of alimentary canal showing clearly thru the thin skin; on segments 7 and 8, two paired, bright

orange bodies which are very conspicuous, these possibly being fatty in nature; welts on the abdomen dark brown; in preserved specimens general coloration fading to a dull yellow.

Form elongate (Plate XX, 57), tapering behind. Surface with a dense, appressed pubescence and scattered erect hairs. Prothorax long, narrowed in front, anterior orifice margined with dense, fine pubescence; sides of prothorax with numerous long, erect, pale hairs. Mesothorax and metathorax indistinctly divided into two approximately equal annuli; anterior annulus with a few lateral setae. First abdominal segment short, the setae arranged as follows: dorsal, two small grouped setae near posterior margin, laterad of each of these, but in alinement, a solitary stout seta, proximad of each of these a stout seta, and cephalad of each of these another strong seta, the principal setae of each side thus forming a rough triangle; a long, delicate pleural seta on each side; ventral, two small groups of setae, with an arrangement similar to that of the grouped setae of dorsum. Abdominal segments 2 to 7 each indistinctly divided into two annuli by a transverse constriction, the anterior ring about half the length of the posterior ring and bearing medially a transverse elongate-oval (dorsal) to short-oval (ventral) welt, covered with microscopic points; ventral welts very convex and swollen; pleura with a long seta; posterior ring with setae arranged as described above for first abdominal segment; setae of posterior segments of body longer, but occupying same relative position; small solitary inner seta of dorsal posterior line becoming large and prominent on seventh segment; segment 8 with six powerful setae in alinement on ventral surface, situated at base of gills, two being pleural and four ventral in position; dorsum of segment 8 with a rounded median lobe. Gills four, long, delicate, divided into lobes by constrictions (the two caudal lobes, as well as the gills, have taken on a respiratory function). Caudal ventral lobes two (Plate XXI, 68) very long, parallel, with scattered setae arranged as follows: at tips, six or seven; at about two-thirds length, three; at about one-third length, a tuft of from fifteen to twenty long and short setae on lateral and dorsal faces; a small solitary seta, dorsal in position, at base of lobe; a similar bristle on ventral face at about midlength of lobe. Like remainder of body, cauda covered with an abundance of delicate appressed pubescence; on dorsal side, at base of each lobe, a rounded spot, and just inside this a narrow, longitudinal line which is destitute of pubescence. Only dorsal lobe the median one of eighth segment, mentioned above. Spiracles lacking.

Head capsule (Plate XX, 58) moderate in size. Lateral plates thin, double, inner one the longest, outer one forming mental plate. Dorsal plate broad in front, narrowed behind, posterior margin bluntly notched; in front of this plate, two broad plates, rather widely separated medially, presumably belonging to clypeus. Labrum broad, cephalic margin and ventral face with transverse rows of short hairs. Mentum (Plate XX, 59) conspicuous, deeply split behind but not entirely divided as in the Pediciini; an outer flattened, circular median lobe whose outer face is covered with small, scalelike roughenings; behind (dorsad of) this outer lobe the mentum proper, roughly triangular in outline, conspicuous, margin with a broad, blunt, median tooth which is sometimes (Plate XXI, 66) bilobed to form two subequal apical teeth; besides this median tooth, four lateral teeth, the outermost one broad with its lateral angle rounded. Hypopharynx (Plate XXI, 64) forming a ring into which ducts of salivary glands open; anterior part, somewhat resembling mentum in shape, a narrow blade with anterior margin having about eight teeth; posterior part a transverse, arcuated band with anterior margin having about twenty teeth. (In the figure, the two parts of the hypo-

pharynx are shown diagrammatically and separated; in some specimens the lateral teeth are more acute, in others they are more rounded.) Antenna (Plate XXI, 65) elongate, cylindrical, chitinized, apex pale, with two long, sensory setae and a few papillae. Mandible (Plate XXI, 63 and 67) strong, flattened, with two powerful bristles on back, or scrobal region, near base; inner face concave, tip ending in a long tooth, dorsad of apex a single smaller tooth, ventral cutting edge with four gradually smaller teeth, beyond the last of which the margin is crenulated into four or five indistinct carunculations; viewed from inside, lateral teeth appearing blunt. Maxilla (Plate XXI, 63) large, consisting of two elongate-oval lobes, the inner one densely hairy; palpus, borne at tip of outer lobe on ventral face, shaped like one-half of a cylinder split lengthwise, several tiny hyaline sense pegs at apex; laterad of palpus and nearer base of outer lobe, a small elongate sensory tubercle with hairs at apex; inner lobe of maxilla subequal in size and length to outer lobe, but more densely hairy; on its ventral face, four or five long sensory tubercles which are expanded at their ends into setiferous heads; at base of maxilla, a long, slender arm with three setiferous punctures at apex and another puncture at about two-thirds length; setae of this arm very long and delicate. (A dorsal view of the larva is shown in Plate XX, 57.)

Pupa.— Length to tip of cephalic crest, 6.2–6.8 mm.
Width, d.-s., 1.4–1.5 mm.
Depth, d.-v., 1.1–1.2 mm.

Head, thorax, and sheaths of appendages dark brown in fully colored individuals; abdomen pale yellowish white; terminal hooks of abdomen heavily chitinized.

Head on margin above eyes with a blunt median lobe and on either side a small but prominent tubercle; gena gibbous. Compound eyes large, semicircular in outline. Front between eyes with margins almost parallel. Labrum with apex truncated or indistinctly bilobed. Labial lobes broad, appearing subtriangular. Sheaths of maxillary palpi not greatly elongated, slender, cylindrical.

Pronotal breathing horns (Plate XX, 61) flattened at base, each arcuated basally behind, bending laterad to form a concave hollow in front; base dark brown, chitinized, branched into eight long, pale filaments which are grouped more or less in pairs; the two ventral and the four dorsal filaments arising from a short common base, the other two being separate for their entire length; these filaments as long as, or longer than, antennal sheaths, varying in length from rather short to a longer type. Thoracic dorsum broad, ample, feebly wrinkled transversely. Leg sheaths (Plate XX, 60) with all the tarsi very long and slender, reaching almost to end of fifth abdominal segment. Wing sheaths comparatively narrow, reaching base of third abdominal segment; anal angle sharp; venation fairly distinct.

Abdomen pale. Intermediate abdominal segments divided into two annuli, the posterior ring much the larger; dorsa of segments 3 to 6 (Plate XXII, 71), and sternum of segment 6, each with basal annulus tumid and with two transverse rows of small hooks converging at the ends to inclose a linear depressed area; these areas capable of contraction, so that the hooks of each row are united or approximated with those of the opposite row; from thirty to thirty-five hooks in each row, anterior row with hooks directed backward, posterior row with hooks directed forward; on seventh segment, only the anterior row of hooks present, very slightly arcuated, the lateral hooks smaller than those near middle of row; caudad of this

row on segment 7, a darkened, transversely rectangular area bearing setiferous punctures in two broken rows, the posterior row the more complete; posterior rings of other segments of dorsum bearing setae in somewhat the same arrangement. Pleural area pale, segments 2 to 8 with a long, delicate seta on each annulus. Dorsum of segment 8 (Plate XXII, 70) with a large setiferous tubercle on either side, this tubercle densely covered with hairs that are longest behind and shorter in front; caudad of these large, blunt knobs, a slender, setiferous tubercle. Last segment with tergal valves chitinized, elongate, extreme posterior margin rounded medially and feebly bilobed, lateral angles produced caudad and dorsad into powerful curved, heavily chitinized hooks; a few setae at about midlength of these hooks (Plate XX, 62). Sternal valves shorter, slightly bilobed medially.

Nepionotype.— Ithaca, New York, June 4, 1917.
Neanotype.— With the nepionotype.
Paratypes.— Topotypic, May 1 to June 10, 1917.

Subtribe **Ellipteraria**

The present knowledge of the immature stages of the genus Elliptera is due entirely to the work of Mik (1886 b). From his rather detailed description and figures, it certainly appears that the group should receive coordinate rank with Antocharia, Limnobaria, and other divisions herein created. The genus Elliptera shows peculiarities of structure in all stages, but many features of its organization remind one forcibly of species of Dicranomyia (such as *D. simulans* and *D. trinotata*) on the one hand, and of Antocha on the other; and it may be that the genus Elliptera stands in closer relationship to Dicranomyia than is now believed.

Genus **Elliptera** Schiner (Gr. *I omit*, or *ellipse* + *wing*)

1863 *Elliptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 222.
1913 *Ellipoptera* Bergr. Ann. Mag. Nat. Hist., 8th ser., vol. 11, p. 576 (correct spelling).

Elliptera is a small genus, including but five species which have a discontinuous range, two being found in Europe and three in western North America. The commonest of the North American species, *E. clausa* O. S., was found on wet moss in the spray of Vernal Falls, Yosemite Valley, California (Osten Sacken, 1877: 198). The only information available on the immature stages of a member of this genus is that furnished by Mik (1886 b) on the European species *E. omissa* Egg. (quoted subsequently by Grünberg, 1910: 31–32, and by Malloch, 1915–17 b: 226–227). The description and account as given below are based entirely on Mik's paper.

Elliptera omissa Egg.

1863 *Elliptera omissa* Egg. Verh. Zool.-Bot. Ges. Wien, vol. 13, p. 1108.

Specimens of *Elliptera omissa* were found by Mik (1886 b) along water-courses and near falls in mountainous regions. The adult flies were noted as late as September 10, swarming about the waterfalls.

Larvae and pupae were found on July 30 and August 17 near Salzburg, upper Austria, living in elongate and somewhat depressed cocoons about 10 millimeters long and 4 millimeters broad which were arranged in longitudinal rows with short spaces between. These cocoons, which were placed with the current, occurred on the wet walls of wooden chutes or runways and also on dripping chalk cliffs. The immature stages spend their existence in these small cocoons of mud and silk. When ready to emerge as an adult, the pupa makes its way thru the end of the cocoon away from the current, leaving the cast skin attached to the opening. The margins of the large pronotal breathing horns of the pupa are finely serrated and are presumably used in making this opening thru the cocoon. The young larva probably creeps about on the floor of the runway, feeding on algae growing in the same situation. When nearly full-grown, the larva crawls to a less exposed place and spins its cocoon. Many larvae and pupae are killed by the drying-out of their haunts when the water supply becomes insufficient to cover them.

Larva.— Length, 7 mm.
Diameter, 1.5 mm.

Body clearly depressed (Plate XXIII, 72), greenish white, scarcely shiny, with delicate appressed grayish hairs which are thicker at the two ends of the body, especially on last segment, where they become almost villous. Integument very transparent, so that intestine and contents show thru, the intestine narrowing on segment 6 and thru to segment 8, where it broadens out and almost entirely fills the ninth and tenth segments. On sides of prothorax a delicate, long, pale hair; on remaining segments two such hairs. On each of abdominal segments 3 to 9, on dorsum near anterior margin, a low transverse ridge which is thickly set with short, blackened points; on sternum of each of same segments, a similar welt which is destitute of points. In male larvae, clawlike appendages of genitalia of adults showing thru skin on ventral side.

Head capsule (Plate XXIII, 73 and 74) massive, slightly longer than broad, black, somewhat shiny, all the sclerites compact and closely united; anterior projecting part of capsule with margins transparent, rust-brown; median part with two small knobs, laterad of which are two larger projections which are crowned with short points; capsule weakly keeled behind on dorsum (Plate XXIII, 74), anterior to which are two swollen elevations; on hinder margin of clypeus a styliform, bristly lobe, easily broken off, which is presumably the antenna.

Labium strongly chitinized, triangular, split longitudinally. Mandible (Plate XXIII, 75) clawlike in appearance, a little smaller than either half of labium, on inner face with a chitinized projection which is serrated. Maxilla indistinct, the palpi coroniform. Spiracular disk (Plate XXIII, 77) with four lobes whose inner faces are narrowly lined with black chitin; lobes provided with lashes of long gray hairs; dorsal lobes the shorter and broader, and bearing on their inner face two elongated stigmata which are margined with pale rust-yellow.

Pupa.— Length, 6.5 mm.

Pronotal breathing horns (Plate XXIII, 76) large, ear-shaped; bright yellowish white in color, in contrast to dirty yellowish brown skin of head, thorax, and appendages; each horn consisting of two parts: the dorsal side, appearing smooth and homogeneous; and the ventral side, with two longitudinal furrows converging toward apices, and with abundant elongate tubercles, under low magnification this part appearing pitted because of the spaces between these tubercles. Margin of breathing horn chitinized and very finely notched. On outer basal part of each ear a parchment-like lobe, which joins ear to side of prothorax; in addition to this, each ear at base is drawn out into an almost rectangular lobe which is closely approximated to pronotum. Leg sheaths extending about to base of fifth abdominal segment. Abdomen distinctly depressed, greenish white in color; segments 3 to 7 on both dorsum and sternum near base with a double cross-row of spicules which present a comblike appearance (Plate XXIII, 78), those on dorsal segments being somewhat stronger. Female pupa with acidothecae grown together on inner face, at outer angle of each a chitinized hook which is curved upward. Male pupa with ventral side of last segment produced into two chitinized points which are bent toward each other and almost touch, these inclosing clasping organs of adult male and hooks of male larva as described above.

Subtribe **Limnobaria**

The subtribe Limnobaria includes about ten genera, which are very closely related to one another and whose limits are as yet not clearly defined. Many of the generic distinctions are based on male characters of wing form, venation, or antennal structure. The genera are often very large and it is difficult to give satisfactory characters to separate their immature stages. The keys to the genera, given below, will unquestionably need much revising when a larger number of forms are studied.

Larvae

1. Form stout; teeth of mandibles and of mentum usually more numerous; mentum more pointed anteriorly .... *Limnobia* Meig. (p. 809)
   Form usually more slender; teeth of mandibles and of mentum usually fewer; mentum transverse or subtransverse 2
2. Mandibles very broad, flattened, with three ventral cutting teeth; mentum about transverse, with nine or eleven teeth .... *Rhipidia* Meig. (p. 825)
   Mandibles more slender, with usually four or five cutting teeth; mentum usually a little pointed anteriorly, with about eleven teeth .... *Dicranomyia* Steph. (p. 819)

Pupae

1. The five basal abdominal segments on both dorsum and venter with a comb of small, blunt teeth; wing sheaths showing an ocellate pattern; pupae living beneath bark of coniferous trees .... *Discobola* O. S. (p. 815)
   Abdominal segments provided with basal transverse welts of microscopic points on segments 3 to 7; wing pattern not ocellate 2
2. Pronotal breathing horns long and narrow, about three times as long as broad. *Rhipidia* Meig. (p. 825)
   Pronotal breathing horns short and broad, length and breadth not greatly different.... 3
3. Size large (usually over 10 mm.); breathing horns often broader than long. *Limnobia* Meig. (p. 809)
   Size smaller (usually under 10 mm.); breathing horns usually as long as broad. *Dicranomyia* Steph. (p. 819)

Genus **Limnobia** Meigen (Gr. *swamp* + *I live*)

1800 *Amphinome* Meig. Nouv. Class. Mouch., p. 15 (*nomen nudum*, preoccupied in Annelida).
1803 *Limonia* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Limnobia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 116.
1818 *Unomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 116.
1856 *Limnomyza* Rond. Dipt. Ital. Prodr., vol. 1, p. 185.

Larva.— Form stout, terete. Abdominal segments with dorsal and ventral transverse welts covered with chitinized points on basal rings. Spiracular disk surrounded by indistinct lobes, the spiracles large. Head capsule large, massive, the dorsal plate narrowed behind and more or less bifid at its tip. Labrum transversely oval, with sensory bristles near margin. Mandible blunt, with from four to seven cutting teeth. Maxilla simple, cardo and stipes large. Antenna with apical papilla button-like. Mentum broad, margin with from eleven to thirteen teeth. Hypopharynx a circlet of two chitinized plates, each with from twelve to fifteen teeth.

Pupa.— No cephalic crest. Pronotal breathing horns flattened, earlike, as broad as, or broader than, long. Mesonotum unarmed. Abdomen with transverse welts of fine hooks on basal annuli of tergites 3 to 7 and sternites 5 to 7. Two tiny spiracles on dorsum of eighth abdominal segment.

Limnobia is a rather small genus (comprising about forty-five species) of usually large and handsome flies. The species are most numerous thruout the Holarctic and Ethiopian regions. The immature stages have a wide range of habitat.

Of the European species, *Limnobia bifasciata* Schr. [= *L. xanthoptera* Meig.] is characteristically fungicolous, the larvae occurring in various species of Agaricus and related genera as stated by Stannius, Pastejrík, De Meijere, and other investigators. *L. decemmaculata* Lw. occurs in fungi (Daedalea and similar species), as recorded by Loew (1873) and by Verrall (1912). *L. quadrimaculata* (Linn.) [= *L. annulus* Meig.] often occurs in tree fungi but is not confined to this habitat. This species,

L. macrostigma Schum., and *L. obscuricornis* Bel. are often found in decaying, principally deciduous, wood. *L. tripunctata* Fabr., *L. sexpunctata* Fabr. [= *L. nigropunctata* Schum.], *L. flavipes* Fabr., and *L. nubeculosa* Meig. are found in humous earth and beneath leaves in woods. The pupal duration of *L. quadrimaculata* is from eight to twelve days, and this species, as well as others of the genus, pupates in the ground, inclosed in delicate silken cases which are covered with particles of earth and other matter.

In America, *L. triocellata* O. S. is characteristically fungicolous. *L. cinctipes* Say, and presumably *L. immatura* O. S., are found both in fungi and in decaying wood. *L. indigena* O. S. has been found in living tulip roots from Greenville, South Carolina (Greene, ms.). *L. fallax* Johns., and presumably *L. solitaria* O. S., live in organic mud near water. *L. parietina* O. S. probably has a similar habitat, since it was found in tent traps set over Beaver Meadow Brook in the Adirondacks (Needham, 1908 a: 171).

Limnobia cinctipes Say

1823 *Limnobia cinctipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21, no. 4.

Limnobia cinctipes is one of the largest and commonest American species of the genus Limnobia. It has been reared many times, some of the records being as follows:

On July 23, 1883, Pergande collected larvae in an old fungus growing on rotten wood. On July 20, 1886, the same species of larvae was found constructing silken cases thru the fungus, and later in the ground for pupation. The pupae were active, and were able to draw back and forth in their tubes. Adults began to issue on July 28, showing the pupal stage in this case to be not more than eight days.

On April 25, 1912, a number of specimens of this species were received from W. H. Shideler, of Miami University, Ohio. The specimens were taken at Oxford, Ohio, on April 20, when several hundred larvae and pupae were found in an old dry log. The young pupae in the wood are not covered with particles of débris, but the older pupae are inclosed in a case which is covered with wood fragments, only the top of the head and the tip of the abdomen projecting beyond the case. When the pupae are about to transform, the insect emerges to about half its length and the

skin splits down the dorsum, the pupal skin remaining in place after the adults have emerged.

On September 15, 1912, many full-grown larvae were found in a fleshy species of Fomes near Gloversville, New York, where they were associated with a much larger number of larvae of *Ula elegans* and a much lesser number of *Limnobia triocellata*. When about to pupate, the larva becomes pale green in color and incases itself completely in a silken sheath which is covered with particles of sand and other débris. As the pupa grows older, the case becomes harder and more rigid. Numerous little mites are to be found running up and down over these pupae, more especially at the head end, and possibly seeking ingress into the insect. One young pupa had a piece of cloth adhering to the side of its case. The pupal stage lasts about five days.

Larva.— Length, 18–22 mm.
Diameter, 2.5–3.2 mm.

Coloration light yellow to greenish, the setiferous transverse welts at base of abdominal segments brownish.

Body terete, abdominal segments subdivided into two narrow basal rings and a broad posterior ring. Abdominal segments 1 to 7 with a broad basal welt on tergites and sternites, that of the first segment much smaller; these welts densely covered with microscopic hooks; on the last two thoracic segments, welts indicated by very narrow lines. Cauda blunt, obliquely truncated. Spiracular disk (Plate XXIV, 83, and Plate XXV, 93) surrounded by indistinct lobes, the ventral margin projecting far caudad and indistinctly divided into two short lobes; lateral lobes very blunt; dorsal lobes short and blunt, often divided into two smaller lobes. Spiracles oblong or elliptical, placed obliquely. Gills four, blunt and rounded, formed for propulsion rather than for respiration.

Head capsule (Plate XXIV, 79) very much as in Antocha, the dorsal plate narrowed behind and somewhat bifid at apex; lateral plates shaped like a mussel shell, curved around to form mentum. Labrum (Plate XXV, 86) distinct, oval, the anterior margin fringed with delicate hairs, the hairs at the lateral margins longer and coarser; on either side near anterior margin, a blunt tubercle with three sensory bristles; just laterad of this a stout seta; along anterior margin, four sensory setae which are subequally spaced. Epipharynx densely hairy. Clypeus broader than labrum, with a seta at each outer anterior angle and two more on either side near posterior margin. Mentum (Plate XXIV, 81) elongate-triangular, not completely divided into halves but deeply split behind, with an outer plate running cephalad into a long, broad point; behind this another plate with the margins toothed, there being about five or six long, acute teeth on either side. Hypopharynx (Plate XXIV, 80) with two rows of teeth forming a circlet, into which duct of salivary gland opens; anterior row having about nine large, blunt teeth, with about six smaller teeth on either side, these latter sharper-pointed and more crowded; posterior row having long, pointed teeth, about twelve in number. Antenna (Plate XXIV, 82) two-segmented, the basal segment chitinized, elongate-

cylindrical, the second segment flattened, shaped somewhat like a door knob; a few sensory projections. Mandible (Plate XXV, 87 and 88) powerful, produced into a strong apical point, with about four or five blunt or irregular inner teeth and a strong dorsal tooth on outer margin before tip. Maxilla (Plate XXV, 87) large, the outer margin thickened, subchitinized; palpi at apex small, shaped like half a pill box, with a few sensory papillae at tip.

Pupa.— Length, 18–20 mm.
Width, d.–s., 2.8–3 mm.
Depth, d.–v., 3.1–3.3 mm.

Entire head and thorax, including leg and wing sheaths, light brown, the thoracic dorsum somewhat darker-colored, the wings more yellowish brown; abdomen pale light green, the segments with the submedian brown band interrupted on pleural region; tip of abdomen brownish, chitinized.

Form stout (Plate XXV, 89); body destitute of noticeable setae.

Head flattened (Plate XXIV, 84). Cephalic crest lacking; forehead with a shallow V-shaped notch between antennal bases. Eyes of male large, the front narrowed, with points of tentorium close to inner margin of eye; eyes of female more widely separated. Antenna rather short, ending just beyond wing root. Labrum short, obtuse. Labial lobes contiguous, divergent, blunt at their tips, posterior margin a little convex medially. Lobes of maxillary palpi large, subquadrate. Cheek with a large, flattened ledge overlying joint of fore legs.

Thorax very gibbous. A distinct anterior median carina between breathing horns. Pronotal breathing horns (Plate XXV, 90) flattened, earlike, broader than long, directed slightly proximad, margin with a row of breathing tubercles, outer face wrinkled. Wing sheaths reaching base of third abdominal segment. Leg sheaths reaching base of fourth abdominal segment or a little longer; tarsi ending about on a level, or sloping gradually from short hind tarsi to long fore tarsi.

Abdominal segments indistinctly subdivided into three rings; on tergites 3 to 7, and sternites 5 to 7, basal ring with a transverse welt which is densely covered with short hairs or hooks, these welts tapering gradually to ends; sternites of segments 3 and 4 having incomplete welts on either side of leg sheaths; band on tergum of segment 7 not broken medially, but a little constricted in some specimens; in older pupae the other annuli, especially the posterior one, variously darkened on dorsum and venter. Female cauda (Plate XXIV, 85) with the acidothecae short, the sternal valves the shortest, the tergal valves a little longer; prominent lateral lobes at base of tergal valves, and a slightly smaller but very broad one on each side of tergal valves at about midlength. Male cauda (Plate XXV, 91) similar to that of female, but the dorsal lobes (Plate XXV, 92) much shorter, not longer than the ventral lobes, and separated by a U-shaped notch; ventral lobes approximated, each ending in a small, blunt tubercle. Two small circular spiracles on dorsum of segment 8, these a little more widely separated in male than in female.

Nepionotype.— Gloversville, New York, October 26, 1912.
Neanotype.— Female pupa with type larva.
Paratypes.— Several larvae and pupae with types and from Oxford, Ohio, April 20, 1912.

Limnobia fallax Johns.

1909 *Limnobia fallax* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 125.

Limnobia fallax belongs to the *solitaria* group and is apparently more Austral in its distribution than the other members of this group (*L. solitaria* O. S., *L. hudsonica* O. S.).

Larvae and pupae were found by Dr. Johannsen near Ithaca, New York, July 20–26, 1905. They were wrapped in silken cases covered with earthy matter, and were removed from the soil near a brook.

Larva.— Length, contracted, 8–8.2 mm.
Diameter, 1.2–1.3 mm.

Coloration white.

Form stout and short, body terete. Transverse welts with chitinized points on abdominal segments 2 to 7, those on dorsal surface broad, those on ventral surface narrower. Spiracular disk blunt, surrounded by four indistinct lobes, the lateral pair the largest and capable of close approximation, closing the large yellow spiracles. Anal gills indistinct.

Head capsule of usual Limnobia type. Labrum (Plate XXVI, 95) broadly oval, lateral angles and disk of epipharynx with tufts of long hairs; anterior margin fringed with short setae; about eight sensory bristles and papillae along anterior margin. Mentum (Plate XXVI, 96) large, triangular, running out into a long median apical point; lateral margins with about six or seven flattened subacute teeth on each side. Hypopharynx as in this group: a collar formed of two chitinized, comblike plates; the first plate rectangular, its face covered with flattened scales, anterior margin with about fourteen acute pointed teeth, the two outermost much the smaller, acicular; the second plate a narrow band of chitin similarly toothed, the teeth at each end large, flattened, the next tooth very narrow, acicular, the remaining teeth, ten in number, flattened, acute, the middle teeth a little shorter and broader. Antenna (Plate XXVI, 97) with basal segment elongate, cylindrical, and apical papilla or segment very tiny, disklike. Mandible (Plate XXVI, 98) large, moderately broad, with apical tooth prominent, two large dorsal teeth, and a row of about five or six comblike teeth along ventral cutting edge, the most basal being short and blunt. Maxilla (Plate XXVI, 99) about as in this tribe, cardines and stipites large and simple; palpus large.

Pupa.— Length of cast pupal skin, 10–13 mm.

Labrum (Plate XXVI, 100) triangular, apex obtuse. Labial lobes prominent, subquadrate. Posterior margin convex medially. Pronotal breathing horns (Plate XXVI, 101) flattened, subcircular in outline, with an outer marginal row of breathing tubercles. Leg sheaths ending just before apex of fourth abdominal segment; tips of tarsi about on a level, or those of fore legs a little the longer. Band of spicules on seventh tergite, slightly constricted medially. Female cauda (Plate XXVI, 102 and 103) with tergal valves a little longer than sternal valves, and more acute at their tips; a small tubercle on outer margin of outer lobes before tips.

Nepionotype.— Ithaca, New York, July 21, 1905.
Neanotype.— Cast pupal skin with type larva.
Paratypes.— One larva and three pupal skins.

Limnobia triocellata O. S.

1859 *Limnobia triocellata* O. S. Proc. Acad. Nat. Sci. Phila., p. 216.

Limnobia triocellata is a common crane-fly in eastern North America. It is closely allied to the European *L. bifasciata* Schr., the immature stages of which have long been known.

Johnson (1906:2) found larvae of this species in a fungus at Riverside, Massachusetts, on August 21, 1904, which pupated on the 22d and emerged on the 30th and 31st, thus giving a pupal duration of about nine days. Malloch (1915–17 b:215–216) found larvae and cast pupal skins in an Agaricus at Urbana, Illinois, in September of 1915. The writer found larvae of *Limnobia triocellata* in a species of Fomes, associated with the larvae of *L. cinctipes* and *Ula elegans*, at Gloversville, New York, on September 15, 1912. C. H. Popenoe found larvae at Great Falls, Virginia, on September 8, 1912, in the fungi *Hypomyces Lactifluorum* (Schw.) Tul. and *Armillaria* sp., the adult flies emerging on October 7, 1912. Other specimens from the same place found on October 9, 1913, in a species of Clitocybe, produced adults on October 20. Scores of specimens were taken in *Boletus felleus* at Bradley Hill, Maryland, the flies emerging on July 16, 1914.

Larva.— Length, 10–18 mm.
Diameter, 1.2–1.4 mm.

Coloration a little more yellowish than that of *Limnobia fallax*. Species very close to *fallax* in all details. Ventral welt on abdominal segment 1 well developed, but dorsal welt lacking or very reduced. Spiracular disk (Plate XXVI, 94) rather large, exposed; circular spiracles large, separated by a distance less than the diameter of one; lobes surrounding disk small and indistinct.

Pupa.— Length, 12–15 mm. Not very different from other species of genus described herein.

Nepionotype.— Great Falls, Virginia, September 28, 1913.
Paratypes.— With the type.

Genus **Libnotes** Westwood (derivation obscure)

1876 *Libnotes* Westw. Trans. Ent. Soc. Lond., p. 505.

Libnotes is a small genus (about thirty-five species) of rather large crane-flies, which are chiefly Oriental in their distribution altho three species occur in South and Central Africa. The species *Libnotes perkinsi* (Grimsh.) has been considered as being a Limnobia, but it seems

to the writer that the present generic reference is more nearly correct, altho the distinctions between Limnobia and some species of Libnotes are very poorly marked. *L. perkinsi* was bred from larvae in damp moss (Perkins, 1913: clxxxii, as Limnobia), and in a letter to the writer Mr. O. H. Swezey states that he has reared this species from larvae in decaying vegetation and in the accumulation of débris behind old leaf-sheaths on banana plants (Musa, Scitamineae) in the Hawaiian Islands.

Genus **Discobola** Osten Sacken (Gr. *discus* + *I throw*)

1865 *Discobola* O. S. Proc. Ent. Soc. Phila., p. 226.
1869 *Trochobola* O. S. Mon. Dipt. N. Amer., part 4, p. 98.

Discobola is a well-marked genus including about eight described species, which are most numerous in the Australasian region, two species only being found in Europe and two others in America. The adults of the commoner American species, *D. argus* (Say), are not rare. They are most numerous in late summer, and are often found resting on the stumps and trunks of coniferous trees, especially white pine (*Pinus Strobus* Linn.).

The immature stages of *D. caesarea* (O. S.) were found by Mik (1884) in Austria, living in decaying pine stumps from which the bark had been removed. The following account is taken entirely from Mik's paper:

Male pupa.— Body cylindrical, slender (9.2 mm. long, 1.5 mm. in diameter). Head, prothorax, mesothorax, leg sheaths, and wing sheaths chitinized, dark brown, shiny, the last-named somewhat brighter than the others, the leg sheaths somewhat darker at their tips. Eyes kidney-shaped, strongly shiny, blackish, between them a small, triangular, blackish brown spot. Prothoracic breathing horns dull-colored, dark rust-brown at base, becoming a brighter rust-brown more distally, compressed laterally, tuberculate, with margin indented. Prothorax carinate, rust-yellow, margined on both sides by dull reddish brown tubercles. In fully colored specimens, forehead and leg sheaths blackish brown, wing pattern indicated on sheaths as somewhat diffused rings. Leg sheaths reaching end of abdominal segment 3, wing sheaths reaching end of abdominal segment 1. Metathorax and abdomen thin-skinned, the former verdigris-colored, the latter white or somewhat yellowish green; metathorax resembling an abdominal segment, but its posterior margin is unarmed, while the first to the fifth abdominal segments on both dorsum and venter bear a comb of very small, short, blunt teeth, which are closely approximated; these teeth chitinized and rusty brown at their tips, giving to abdomen the appearance of having brown incisions; these transverse rows of teeth interrupted at pleura. Sixth abdominal segment pale thruout and lacking the comb. Seventh segment shorter and narrowed on dorsum, pale, bearing on sternum a rust-yellow chitinized plate which is narrowed anteriorly, leaving an uncolored triangular area on either side at base of segment. Eighth segment swollen to include genitalia, the

two basal parts ellipsoidal, strongly shiny, rust-yellow, somewhat darker at tips, the apical parts small and knotlike, bluntly rounded; segment bearing on dorsum a weak triangular piece at its base; between apical parts of genitalia are inserted two small chitinized shields; on venter, between basal parts, sheath of penis is inserted.

Female pupa.— Body resembling that of male, but longer and somewhat stouter (length 10.5 mm., diameter 1.8 mm). Leg sheaths extending to just beyond midlength of abdominal segment 2. Seventh abdominal segment shortened and somewhat narrowed, on dorsum largely pale, with a narrow chitinized margin only on lateral parts, so that the unchitinized part forms a triangle with the apex directed backward; on sternum this segment almost completely chitinized, rust-yellow, only a small triangular area at base on either side remaining uncolored; chitinized plate separated from plate of next segment only by an incomplete segmentation, swollen, and bearing two longitudinal impressions. Eighth segment bearing on its dorsal surface the dorsal valves of ovipositor, fused at their base, chitinized thruout, rust-yellow in color; segment bearing on its ventral surface a depressed conical chitinized plate of a rust-yellow color, and with transverse impressed wrinkles; on either side a small, dark, chitinized, lower valve of ovipositor. Other characters as in male. (When the pupae are placed in alcohol, the green of the metathorax and the abdomen disappears and is replaced by a yellowish white color.)

Pupae were collected in large numbers in a pine wood near Hammern in Freistadt (upper Austria) in the latter days of August, 1882. The pupae live in pine stumps, near the ground, where the bark has been removed, more especially in situations where the wood is somewhat sappy and not yet completely decayed. Those found were not deep in the wood. Their presence was discovered by finding the teneral adults on and near a stump, and many cast skins of the pupae projecting horizontally, the caudal end of the body, up to the leg sheaths, adhering to the wood. No emergence holes were found on the cut surface of the stump. The adults at first have a very long, pale abdomen, which is of a verdigris color, most intensive at the base and paler toward the tip. The pupae that were found transformed as adults in from one to three days.

Genus **Geranomyia** Haliday (Gr. *crane* + *fly*)

1833 *Geranomyia* Hal. Ent. Mag., vol. 1, p. 154.
1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, vol. 4, p. 683 (spurious name).
1838 *Aporosa* Macq. Dipt. Exot., vol. 1, part 1, p. 62.
1865 *Plettusa* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 597.

Geranomyia is a rather extensive genus including about eighty species, which are most abundant in the tropics of America, Asia, and Australia. On the African continent the genus is apparently less common. The adult flies have an elongate rostrum which is used for sucking nectar

from tubular flowers. The various species of the genus have been recorded as feeding on a wide range of plant species, which have been indicated by Knab (1910) and by Alexander (1916 b:486–493) and may be summarized as follows:

Species	Plants frequented
Geranomyia canadensis	Compositae — Eupatorium, Solidago, Aster, Silphium, Rudbeckia, Verbesina, Cacalia, and similar species
Geranomyia diversa	Compositae — Solidago, Erigeron Umbelliferae — Daucus
Geranomyia virescens	Lauraceae — Persea
Geranomyia rostrata	Compositae — Eupatorium, Solidago, Helianthus

For many years nothing was known concerning the immature stages of any species of Geranomyia. In 1917, J. R. Malloch found larvae and pupae of *G. canadensis* at Urbana, Illinois. Mr. Malloch and the writer have in press a detailed paper on the immature stages of this species, and the following brief account is abstracted from this paper and included herewith in order to complete the data.

Mr. Malloch found the larvae on the grounds of the Floriculture Department of the University of Illinois. There is a small bubbling fountain here, the waste water from which flows along an open gutter. In this gutter the immature stages of *G. canadensis* lived among the vegetable growth and diatomaceous ooze in the bottom of the trough. Mr. Malloch and the writer found this same species in Union County, southern Illinois, in 1919. Here larvae and pupae occurred on the face of rocks where the surface was continually damp with percolating water. A railroad bank had been formed by piling up slabs of limestone to a height of about four feet. In the irregularities and crevices of these pieces of limestone, the larvae of Geranomyia were living in delicate silken tubes covered with a deposit of silt and diatoms. They emerged from their cases to feed on the exposed surface of the wet rocks during twilight, and even during the hours of sunlight, but upon being disturbed or alarmed they retreated with great agility into their tubes. The pupae are found in short, nearly vertical burrows in the same situations as the larvae; here they rest with only the long, conspicuous breathing horns projecting from the entrance to the burrow. When transformation takes place, the pupal skin projects from the mouth of the burrow nearly to the ends

of the wing sheaths. The number of larvae vastly exceeds the number of pupae, and this would seem to indicate that the pupal existence is of very short duration, else this stage would be found oftener.

Larva.— Length, 12–12.5 mm.
Diameter, 0.8–0.9 mm.

Coloration grayish subhyaline; a large orange area on posterior lateral parts of prothorax; abdominal welts dark brown.

Form moderately long and slender; thoracic segments gradually decreasing in length from prothorax to mesothorax; abdominal segments gradually elongated to the fifth, thence shortened to end of abdomen. Ventral surface of meso- and metathorax and of first eight abdominal segments provided with a basal transverse welt which is densely set with microscopic points; on dorsal surface these bands smaller, occurring on metathorax and on abdominal segments 2 to 8, not connected with sternal bands except on metathorax and on eighth abdominal segment. Spiracular disk similar to that in Dicranomyia; the usual ventral lobes represented only by two small, dusky, setiferous areas. Spiracles large, elongate-oval, placed obliquely on the sides of a deep split and so capable of close approximation. Anal gills four, each short, tapering gradually to the blunt tip.

Head capsule compact, massive, as in tribe. Labrum transversely oval, margin with short yellowish hairs and a larger tuft on either side. Antenna two-segmented, second segment rather stout, cylindrical, slightly arcuate; apical papilla small but high. Mandible broad and flattened, with a small dorsal tooth and a row of five ventral teeth. Maxilla generalized in structure, as in tribe. Hypopharynx as in Limnobaria, consisting of a roughly circular chitinized collar provided with a crown of stout teeth. Mentum broad, undivided, anterior margin with eleven teeth.

Pupa.— Length (including breathing horns), 8–9 mm.
Length of breathing horns, 1.2–1.3 mm.
Width of body, d.-s., 0.85–0.9 mm.
Depth, d.-s., 1–1.05 mm.

Pronotal breathing horns grayish subhyaline; head and thorax with sheaths dark brown; abdomen whitish, hooks and spines brown.

Cephalic crest small, indistinctly bilobed, not setiferous; front long and parallel; rostral sheath very long and narrow, subtended on either side by sheaths of paraglossae, the latter projecting beyond tip of rostrum and ending almost opposite end of wing sheath; margin of cheeks flattened as in Limnobaria. Antennal sheaths short, ending slightly beyond base of wing pad. Pronotal breathing horns very large and prominent, not contiguous basally; about a dozen breathing pores along dorsal margin. Mesonotum unarmed; wing sheaths ending opposite base of third abdominal segment; leg sheaths ending opposite or slightly beyond midlength of fourth abdominal segment; tarsal sheaths ending about on a level. Abdominal segments 3 to 7 near base with two bands of chitinized hooks arranged in curved transverse rows inclosing an oval transverse area. Cauda chitinized, tergal region produced into two parallel curved hooks bending strongly dorsad.

Found at Alto Pass, Union County, Illinois, June 6, 1919.

Genus **Dicranomyia** Stephens (Gr. *fork* + *fly*)

1818 *Furcomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 106 (*nomen nudum*).
1829 *Dicranomyia* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Siagona* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, pl. 65, figs. 5–7.
1830 *Glochina* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 280.
1854 *Numantia* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 2, p. 470.

Larva.— Form slender. Body nearly glabrous, abdominal and thoracic segments with dorsal and ventral transverse welts on basal annuli. Spiracular disk small, the five lobes indistinct but indicated, spiracles large. Anal gills four, slender. Head capsule massive, of the Limnobia type. Mouth parts almost as in Limnobia; ventral cutting edge of mandible with fewer teeth; mentum with anterior margin more transverse and with fewer teeth.

Pupa.— Cephalic crest lacking. Pronotal breathing horns broad, in *D. simulans* with a basal recurved hook on dorsal side, in other known species unarmed. Basal abdominal annuli with transverse welts. Dorsum of eighth abdominal segment with vestigial spiracles.

Dicranomyia is a very extensive genus including more than two hundred described species of usually small flies which are found in most parts of the world. The immature stages, which are found in a variety of habitats practically as extensive as is covered by the entire family of crane-flies, range from forms that are almost strictly aquatic, thru species living beneath the bark of trees, to still other species which are leaf miners.

In Europe, *Dicranomyia trinotata* (Meig.) is a characteristic member of the hygropetric association, the insects living on rocks in streams, where they are covered with a thin sheet of water and are usually associated with such insect forms as Beraea, Tinodes, Stactobia (Trichoptera), *Orphnephila testacea* (Ruthe), *Pericoma nubila* (Meig.), *Dixa maculata* Meig., *Oxycera pulchella* Meig., and other Diptera. The larva is cylindrical, measuring from 10 to 11 millimeters in length and from 1.5 to 2 millimeters in diameter. The dorsal surface is greenish mottled with darker, the ventral surface brighter. The larvae live in loosely spun silken cases in which they pupate. The pupae are about 10 millimeters long, and live in cocoons which are almost horizontal in position. The mature pupa breaks thru the cocoon by means of its sharp-edged breathing horns, the adult then creeping forth and leaving the cast pupal hull behind. (Thienemann, 1909:64–65, and Grünberg, 1910:29.)

Dicranomyia dumetorum Meig. lives in decaying, principally deciduous, wood. Winnertz (1853) found it in large numbers in a decaying beech tree, associated with *Bremia cilipes* (Winn.).

A species of crane-fly doubtfully referred to *Dicranomyia pilipennis* Egg. (Schubart, 1854) has been found in ditch water in Holland.

Dicranomyia umbrata de Meij., a Javan species, lives in the slimy green algae floating in stagnant, as well as flowing, water. The pupae live in cocoons in the algal sheath, with the cephalic end projecting. The larvae are from 10 to 12 millimeters in length, cylindrical, about 0.6 millimeter in diameter, and of a yellowish color. The head is almost entirely retractile. The body is almost smooth, having only an inconspicuous transverse welt on the second abdominal segment near the posterior margin. The caudal end is somewhat enlarged and is truncated behind. De Meijere (1916:197–198) supplies a good description of the structure of the larval head capsule.

Dicranomyia foliocuniculator Swez., of the Hawaiian Islands, is the only recorded leaf-mining crane-fly. It was found by Swezey mining in the leaves of a species of Cyrtandra (Gesneriaceae) in the island of Oahu. Pupation of the species takes place within the mines (Swezey, 1913 and 1915).

In North America a number of species are known. *Dicranomyia simulans* has been ably discussed by Needham (1908a:214–217) and later by Malloch (1915–17b [1917]). This species is, for the most part, a member of the hygropetric fauna, dwelling in usually lotic water where it is associated with a characteristic rapid-stream fauna. Other conditions under which the species is found are discussed later. *D. badia* and *D. stulta* live in and under saturated moss cushions. *D. macateei* Alex. has been bred from larvae in decaying wood (Dr. W. G. Dietz). *D. rara* O. S. has been bred from larvae in a rotten willow, the larvae being taken on Plummers Island, Maryland, by H. S. Barber on October 12, 1913, and emerging as adults on November 14.

Dicranomyia simulans (Walk.)

1848 *Limnobia simulans* Walk. List Dipt. Brit. Mus., vol. 1, p. 45.

The best account of the life history of the common and widespread *Dicranomyia simulans* is that by Needham (1908a:214–216), quoted below:

> It is abundant on the piers along the west shore of Lake Michigan. . . . This pier [at Lake Forest, Illinois] was built on heavy driven piling, covered outside with heavy plank. About three feet of surface was exposed above the water at its normal stage. The planks were old, and sheltered a scanty growth of short, stemmed mosses in the cracks, and bore

a heavy fringe of Cladophora and other algae just below the water line, with a film of " skin algae " extending a little higher.

All over the sides of the plank, in either sun or shade, the adult *simulans* could be seen throughout the summer months, sometimes in considerable numbers. I was first attracted to notice them by their habit of running rapidly sidewise along the pier, and their resemblance to harvestmen (Phalangidae). They run habitually sidewise, apparently rarely moving forward except to escape an obstruction, and very rarely appearing on the top of the pier. They rest in an inverted position on the under surface of the overhanging plank on the top of the pier. They stick to the surface so persistently that it is difficult to make one take flight; they may be driven all about on the surface, or poked with a stick; they can fly well enough when they will, but when induced to fly they settle again almost at once, and within a few feet of their starting place.

They are associated upon the piers with *Geranomyia canadensis* and with numerous midges and micro-caddis flies (Hydroptilidae) and a few larger caddis flies of the genus Hydropsyche.

Males are more in evidence, but probably not more abundant in fact. The females come out from their resting places only to lay their eggs, and are only to be seen when busily engaged in the performance of this task. They stand on tiptoe, with the long ovipositor held in vertical position at the tip of the deflexed abdomen, and they swing the body up and down in rapid shuttlelike vibration, freely rising and falling on the long and widely outspread legs. Thus the point of the ovipositor is driven against the wet surface of the plank, thrusting almost as rapidly as the needlebar of a sewing machine; it is moved about over the surface, as if searching for soft spots in the wood, and occasionally it makes a deeper thrust when a suitable place is found, and an egg is deposited.

The egg-laying process is often interrupted and is continuously interfered with by the too importunate males. When a male in running about on the plank comes upon a female ovipositing, he stands directly above her at the full upward stretch of his legs, while she goes right along with her work; but the instant she ceases her vibrating and lifts her ovipositor, he is ready with his forceps, upturned and outspread at the tip of his decurved abdomen, to seize her. Usually she does not want to be interrupted and moves away, while he tries to run parallel and maintain all the while his position of vantage above her. Often other males are encountered, and then the males engage in a rough and tumble fight. They push and shove each other in a most ludicrous manner, reminding one of pigs fighting, and often an encounter of this sort enables the female to escape and go on quietly with her work.

The males have well developed eyes, but their sight must be very poor; for, while always searching for females, they seem quite unable to find them by sight, often passing females at work within a distance of a few centimeters. But their tactile sense seems more acute. When a male in running to and fro had passed several times within six centimeters of a female without noticing her, was deflected from his course toward her by an obstruction I purposely placed in his way, he instantly sprang toward her upon the slightest contact, even of tips of tarsi, but was quite unheeding until this contact occurred. If it did not occur he would pass on, even by the narrowest margin.

All stages are found together on the piers. The eggs are laid in the soft spots in the old wood, where the surface of the pier is kept wet, but not continually covered by water, in the zone of the " skin algae." The larvae live exposed or thinly algae covered, and crawl about slowly over the wet surface. They are greenish in color and very inconspicuous. In a cavity among the stems of the dwarf mosses (*Bryum binum* Schoeb. var. *varium* Lindb. and *Amblystegium orthocladon* Lesq. and James) in a crevice at the upper limit of the wet area the larva spins about itself a sheet of tissue and fastens bits of moss stems and leaves to its outside, and transforms inside the tube thus formed into a pupa. The tube is longer than its body, and the pupa moves in or out at will, doubtless by the aid of the hooks at the ends of its body.

The following descriptions of the immature stages are adapted from those of Needham and Malloch:

Larva.— Length, 10–15 mm.
Diameter, 1.5–2 mm.

Coloration green, with distinct brown marks on dorsum and with an interrupted mid-dorsal row of alternating paler dots and crossmarks; dark area made up of closely placed spinous hairs, clear areas for the most part devoid of hairs.

Body cylindrical, abruptly tapering behind on last abdominal segment. Legs lacking, but a scurfy, pubescent creeping-fold on under surface of meso- and metathorax, a similar one on first abdominal segment, and much larger, transversely placed, fusiform creeping-ridges on ventral surface of abdominal segments 2 to 7, on anterior ring of each segment. Incisions between dorsal segments of abdomen margined with blackish spinules, which are slightly stronger than other hairs of dorsum. Spiracular disk vertically cleft, with sloping sides, folded together when under water, border of aperture fringed with short hairs and destitute of fleshy lobes. Spiracles oval. Anal gills four, fleshy.

Head large, similar in general appearance to that of Limnobia, entirely retractile within enlarged prothorax; head showing a broad, pale yellow, median band, sides black from base of antennae backward. Labrum transversely oval, with a margin of close-set, scurfy hairs; clypeus one-fourth broader than labrum, yellow, with parallel sides but emarginate on front for reception of labrum; three recurved, stout setae on lateral margin of clypeus on each side, one on each angle and two on disk. Mentum slightly convex in outline, median tooth much longer and stouter than first lateral, second and third laterals as large as median tooth. Antenna long, the shaft about three times as long as its greatest diameter. Maxillary palpi short and inconspicuous.

Pupa.— Length, 8–9 mm.
Diameter, 1.5 mm.

Body smooth and shiny, ends brownish. Front of thorax upcurved dorsally. Pronotal breathing horns broad, laterally flattened, obtuse at apex, each with a basal recurved, sharp hook on its dorsal side; breathing tubercles arranged in a semicircular row along obtuse tip of horns. Dorsum of thorax with a faint fretwork of raised lines on surface. Abdomen smooth, with transverse lines of scurfy pubescence, terminating in a pair of stout, sharply recurved hooks.

Malloch (1915–17 b, pl. 33, fig. 5) has figured the peculiar pronotal breathing horn of this species.

Dicranomyia stulta O. S.

1859 *Dicranomyia stulta* O. S. Proc. Acad. Nat. Sci. Phila., p. 210.

Adults of *Dicranomyia stulta* are often exceedingly abundant, flying about, or resting in close proximity to, rocky ledges or cliffs near streams. They are found commonly in June, associated with such crane-fly species

as *Geranomyia canadensis, Dactylolabis montana, Tipula ignobilis, T. apicalis*, and similar forms. The larvae live in and beneath the saturated cushions of moss (Amblystegium) that grow on the shale near the water's edge. The only associated crane-fly larvae found near Cascadilla Creek, Ithaca, New York, where this species is common, were *Tipula ignobilis*, the larvae of both species being exceedingly abundant.

Larva.— Length, 10-12.2 mm.
Diameter, 0.6–0.7 mm.

Color pale whitish with a green cast; transverse abdominal welts dark brown.

Form rather long and slender. In addition to dorsal and ventral welts on abdominal segments 2 to 8, a complete band at base of metathorax and ventral bands on mesothorax and first abdominal segment; ventral abdominal bands larger and more conspicuous than narrow dorsal welts. A few erect setae on body. Spiracular disk (Plate XXVII, 105) rather small, with a deep vertical split, the large ovate spiracles capable of close approximation; ventral lobes blunt, with a black spot on face, fringed with short black hairs and with two sensory setae; each blunt lateral lobe narrowly lined with a black crescent; dorsal lobes very small, dusky; spiracular disk fringed with short, dark hairs. Anal gills four, large and pale.

Head capsule as in tribe. Labrum (Plate XXVII, 106) subtriangular; anterior margin broad, nearly straight across, with a dense fringe of hairs which are coarser at ends of lobe; near anterior margin of labrum two oval, hyaline areas, each with three short papillae; a few sensory setae along anterior margin. Mentum (Plate XXVII, 107) broad, anterior outline triangular, running out into a rather long apical point, each side with about five teeth. Hypopharynx (Plate XXVII, 108) as in this group of genera, consisting of a collar of two chitinized combs, each with about ten sharp teeth. Antenna (Plate XXVII, 109) short, cylindrical, the apical papilla very small, reduced to a tiny disk. Mandible (Plate XXVII, 110) broad, flattened, with a blunt apical point which is only a little longer than the teeth on either side of it; ventral cutting edge with about five blunt teeth, which are gradually smaller from the outermost toward the base; inner face of mandible with a blunt prosthecal tooth and an oblique fringe of coarse setae. Maxilla (Plate XXVII, 111) with the cardines large, with about three setiferous punctures; stipites short, cylindrical; outer lobe fringed with long hairs and bearing the short, flattened, disklike palpus, which has five or six hyaline pegs; inner lobe smaller, with dense, short hairs and a few sensory organs.

Pupa.— Length, about 6 mm.

Labrum very obtusely rounded at apex, not bilobed. Labial lobes straight across or very slightly convex across posterior margin. Maxillary palpi narrowed toward tips (Plate XXVIII, 112). Pronotal breathing horns (Plate XXVIII, 113 and 114) elongate-oval, earlike, the ventral margin more bulging, the apex a little narrowed but obtuse; a row of breathing pores along outer margin, beginning on lateral face near dorsal margin, these few in number and widely separated, becoming more numerous toward apex of organ. Leg sheaths as usual in this group of genera, those of fore legs the longest, those of hind legs the shortest. Male cauda (Plate XXVIII, 115) with ventral lobes (Plate XXVIII, 116) large, bluntly rounded at tips; two small, brown, approximated tubercles at base of split on

ventral side; two blunt tubercles on dorsal surface near base and close to median line (Plate XXVIII, 117). Tergal lobes at outer angles of a flattened plate, very short, triangular, each with two small hairs on caudal face before tip.

Nepionotype.— Cascadilla Creek, Ithaca, New York, May 22, 1917.
Neanotype.— Type locality, June 6, 1917.
Paratypes.— Abundant larvae and pupae with types, May 22 to June 6, 1917.

Dicranomyia badia (Walk.)

1848 *Limnobia badia* Walk. List Dipt. Brit. Mus., vol. 1, p. 46.
1859 *Dicranomyia humidicola* O. S. Proc. Acad. Nat. Sci. Phila., p. 210.

Dicranomyia badia is a very common species thruout eastern North America, occurring in gorges and ravines and along streams. The adult flies may be found resting on perpendicular cliffs near these haunts. In a position of rest they have all six feet on the support, a very different resting position from that of the often-associated genera Oropeza and Dolichopeza.

The larvae, as is frequent in this genus, live in and beneath moss, especially saturated cushions of moss growing in or near the margins of streams. They are of a clear light pea-green color, and simulate the moss to an astonishing degree. The writer found these larvae in Needham's Glen, Ithaca, New York, on April 16, 1917, beneath wet cushions of *Amblystegium irriguum* (Hook. & Wils.) B. & S., a moss that covers all the rocks and stones near water. In these moss cushions the larvae were associated with tiny larvae of *Tipula ignobilis* and pupae of *T. collaris*. When ready to pupate, the larva spins a small, silken, silt-covered case, which is further protected by a covering of small pieces of moss stems adhering to its outside, this case being hung up in the moss cushion, with the cephalic end of the pupa projecting. The pupal duration is about seven days (April 21 to 28 in the cases observed). The dark-colored pupa, with its contrasting yellow breathing horns, is very handsome.

Larva.— Length, 10.5 mm.
Diameter, 0.6–0.65 mm.

Coloration light pea-green, abdominal welts brown; after death general color fading to very pale greenish white.

Form slender; body terete, dorsal and ventral transverse welts at base of abdominal segments conspicuous. Spiracular disk (Plate XXVII, 104) with lobes indistinct, suffused with dusky, lateral lobes very blunt; disk surrounded by a fringe of short, dark-colored hairs. Spiracles very large, ovate, dorsal ends close together. Anal gills long and slender, pale.

Head capsule and mouth parts similar to those of *D. stulta*, already described, judging from the scanty material of *D. badia* available for study.

Pupa.— Length, 8–8.5 mm.
Width, d.-s., 1.1 mm.
Depth, d.-v., 1.2 mm.

Head, thorax, and appendages dark brown; pronotal breathing horns light yellow; abdomen greenish, the cauda chitinized, light brown.

Labrum very broad, indistinctly bilobed at tip. Labial lobes large, broadly transverse, posterior margin almost straight across. Maxillary palpi broad, tips truncated (Plate XXIX, 119). Lateral margins of cheeks flattened into ledges.

Pronotal breathing horns large, flattened, in lateral outline (Plate XXIX, 118) subcircular or nearly so, with a row of rather widely separated breathing tubercles along margin; as viewed from above, horns directed proximad, so as to be contiguous at tips. A high median crest on mesonotum behind breathing horns. Wing sheaths ending before apex of abdominal segment 2. Leg sheaths ending far before apex of abdominal segment 4; as usual in this division, the hind legs a little the shortest, the fore legs a little the longest. Abdominal segments with a distinct basal welt which is thickly margined with microscopic curved hooks. Lateral spiracles distinct, but small and probably nonfunctional. Female cauda with sternal valves shorter than long tergal valves, the latter (Plate XXIX, 120) almost straight, each with a powerful, acute spine on lateral margin at about midlength, this directed dorsad. Near the margin of segment 8, on dorsum, a pair of rudimentary spiracles.

Nepionotype.— Needham's Glen, Ithaca, New York, April 16, 1917. (No. 5–1917.)
Neanotype.— Type locality, May 7, 1917.

Genus **Rhipidia** Meigen (Gr. *a fan*)

1818 *Rhipidia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 153.
1911 *Ceratostephanus* Brun. Rec. Indian Mus., vol. 6, p. 271.

Larva.— Form rather stout, body terete. Abdominal sternites 1 to 7 and tergites 2 to 7 with narrow transverse basal welts of chitinized points. Spiracular disk with indistinct lobes. Head capsule massive, not unlike that of Dicranomyia. Labrum broadly transverse. Mandible very broad, flattened, with only three ventral cutting teeth. Maxilla of simple structure. Antenna with apical papilla or segment very flattened, disklike. Hypopharynx of two chitinized plates, each with about twelve comblike teeth. Mentum almost transverse across anterior margin, with from nine to eleven teeth, the outermost fused.

Pupa.— Pronotal breathing horns elongate for this subtribe, about three times as long as broad. Abdomen with transverse bands of spicules on tergites 3 to 7 and sternites 5 to 7, and on extreme lateral parts of sternites 3 and 4.

Rhipidia is a small to medium-sized genus (about thirty-five species) having its center of distribution in the American tropics, with some species occurring thruout temperate Europe and America and a less number in Africa and the Oriental region. The genus is based on a sexual char-

acter, the pectinate antennae of the male, and several of the species run inconveniently close to Dicranomyia.

The immature stages are spent beneath the bark of decaying trees or in decaying vegetable or animal matter. In Europe the genotype, *Rhipidia maculata* Meig., has been recorded as living in old cow-manure. Beling found the insects in such a situation, associated with the larvae of *Rhyphus punctatus* (Fabr.) (Beling, 1879:52–53) and a staphylinid beetle, *Platystethus morsitans* Payk. (Beling, 1873 b:592). *R. uniseriata* Schin. was found by Beling (1879:53–54) living in decaying beech wood, in company with larvae of *Xylota lenta* Meig. and *X. segnis* (Linn.) (Syrphidae) as well as with larvae of a tipuline crane-fly, Ctenophora. The larvae of this species, like those of *R. maculata*, live in thin silken cases, open at both ends and covered with particles of wood and other débris.

In America, besides *Rhipidia bryanti* (which is discussed in some detail) the following records of the immature stages are available: *Rhipidia maculata*, recorded in Europe as living in decaying organic matter, was found by Needham (1908 a:170, 204) in tent traps set over the bed of Beaver Meadow Brook in the Adirondacks, the insects presumably having emerged from the stream bed or from the thin layers of moss covering the exposed stones. *R. fidelis* O. S. was reared from larvae in decaying wood near Ithaca, New York, by Carl Ilg. This species belongs to the same subgenus (Monorhipidia Alex.) as the European *R. uniseriata*, which has similar larval habits. *R. domestica* O. S. has been bred from larvae obtained in fermented sap of the sour gum (*Nyssa sylvatica* Marsh., Cornaceae) at Clementon, New Jersey (Johnson, 1910:704). Males and females of this species were bred by Popenoe at Washington, D. C., from larvae on more or less decaying roots of taro (*Colocasia antiquorum* Schott, Araceae) taken at Gough, South Carolina, on February 1, 1911. Specimens of *R. domestica* emerged on August 21, 1906, at Juneau, Alaska, in radishes infested with *Hylemyia brassicae* (Bouché).

Rhipidia (*Rhipidia*) *bryanti* Johns.

1909 *Rhipidia bryanti* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 123–124, pl. 16, fig. 20.

Rhipidia bryanti is one of the largest and handsomest species of the genus, and is widely distributed thruout the eastern United States from Maine to Texas. The immature stages are spent beneath the decaying

bark of trees. The material studied was collected by J. R. Malloch in Potomac Park, Washington, D. C., on May 11, 1913, and was reared by R. C. Shannon (No. 35–1913), whose notes on the subject are as follows:

A small colony (about seven) of tipulids were found in a hollow of a tree behind the bark. The larvae were covered with slime, which gathered débris as they moved about and so formed a case. The next morning one had pupated. Two larvae were boiled and preserved in alcohol, while two others were preserved in formal. As they move about they leave a path of slime behind them. On May 14, the one that had pupated on the 12th emerged. On May 18 another imago issued.

There is an obvious error in the duration of the pupal stage as given — only two days. It is possible that a pupa was included in the material and was overlooked in its case of débris. The date of emergence of the second adult would show a pupal duration of six days, which is probably nearly correct.

Larva.— Length, 13.2–14 mm.
Diameter, 1 mm.

Coloration white.

Form terete, rather stout. Sternites 1 to 7 and tergites 2 to 7 with narrow transverse welts on basal rings; welts yellow, provided with long, transverse rows of microscopic roughened points, those along margins of welts coarser, those in centers very tiny; these rows interrupted along pleura. Caudal end blunt, with lobes of spiracular disk indistinct. Spiracles large, capable of close approximation.

Head capsule massive, of the Limnobia type. Labrum (Plate XXX, 121) broadly transverse, anterior margin almost straight across, near margin two oval areas which are provided with small sensory papillae. Epipharyngeal region with abundant hairs. Mentum (Plate XXX, 122) chitinized, the anterior margin almost transverse, with a large median tooth and about three lateral teeth on either side, the outermost of these an evident fusion of about three lesser teeth. Hypopharynx (Plate XXX, 123 and 124) as usual in this subtribe, a collar-like structure composed of two parallel combs united at the ends; the larger plate broadly elongate, surface with abundant scalelike plates, anterior margin with twelve teeth, the lateral ones narrow, the teeth gradually enlarging toward the middle, the middle pair a little shorter; second plate of hypopharynx broadly transverse, narrow, likewise with about twelve teeth, the two outer most on each side long, subacute, the middle tooth shorter and more flattened; between the two middle teeth a small triangular or conical point. Antenna (Plate XXX, 125) short cylindrical, the apical papilla a very flattened disk or button which is much broader than long. Mandible (Plate XXX, 126) very broad, flattened, with the apical tooth rather long and slender; two smaller teeth dorsad and three others ventrad, the dorsal teeth blunt, the ventral teeth truncated, the most basal tooth very broad. Maxilla (Plate XXX, 127) of the simple generalized structure of this tribe; cardines large, with two setiferous punctures; stipites weakly chitinized basally; outer lobe of maxilla with the large flattened palpus at its tips; palpus surrounded by numerous long setae and having several hyaline sense pegs at its apex; inner lobe of maxilla smaller, with numerous long hairs, especially a slitlike brush near margin.

Pupa.— Length, about 12 mm. (cast skin).

Labrum broad, rounded at apex. Labial lobes broadly transverse, caudal margin indistinctly trilobed. Maxillary palpi large, flattened, apex bluntly pointed; a rather angular tooth on margin near base (Plate XXXI, 128). Cheeks produced into flattened ledges. Antennae short and stout.

Pronotal breathing horns (Plate XXXI, 129) elongate for this subtribe, about three times as long as the greatest diameter, flattened, apical half slightly expanded, margin with tiny tubercles. Wing sheaths attaining base of abdominal segment 3. Leg sheaths attaining base of abdominal segment 5; tarsi ending about on a level, or hind tarsi a little the shorter and fore tarsi a little the longer. Abdomen with basal bands of setae on tergites 3 to 7 and sternites 5 to 7, and on the extreme lateral parts of sternites 3 and 4; these bands thickly margined with tiny, golden-yellow hairs or points, the median part of each band naked or nearly so. Male cauda (Plate XXXI, 130) with dorsal lobes (Plate XXXI, 131) very small, more or less flattened, divergent, rather blunt at tips; ventral lobes elongate, contiguous along inner face.

Nepionotype.— Potomac Park, D. C., May 11, 1913.
Neanotype.— Cast pupal skin, with type larva, May 14, 1913.
Paratype.— One larva with type.

Subtribe **Dicranoptycharia**

The subtribe Dicranoptycharia, so far as known, includes only the genus Dicranoptycha. The division is close to the Rhamphidaria but is easily separated from it in all stages.

Genus **Dicranoptycha** Osten Sacken (Gr. *fork* + *fold*)

1818 *Marginomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 147 (*nomen nudum*).
1859 *Dicranoptycha* O. S. Proc. Acad. Nat. Sci. Phila., p. 217.

Larva.— Form very elongate, terete. Integument smooth, glassy, transparent. Abdominal segments 2 to 8 each with a basal transverse band or area of microscopic chitinized points on ventral surface; segment 8 with a similar band on dorsum. Spiracular disk surrounded by four lobes, the lateral pair more slender than the blunt ventral pair; dorsal lobe very low or lacking; a triangular brown mark on disk between spiracles. Spiracles small, widely separated. Anal gills a fleshy protuberant ring surrounding anus.

Head capsule compact, massive, the prefrons large with a few marginal punctures; externolateral plates very broad. Labrum large, flattened, pale. Antenna two-segmented; apical segment almost as long as basal segment, gradually narrowed to the blunt tip. Mandible with a blunt dorsal and two blunt ventral teeth. Maxilla generalized in structure. Hypopharynx a rounded cushion. Mentum deeply split behind but not completely divided, with three principal teeth and a small reduced lateral tooth on either side.

Pupa.— Cephalic crest low, depressed, setiferous. Labrum tumid. Labial lobes oval, contiguous. Antennal sheaths ending opposite base of wing pad. Pronotal breathing horns microscopic, represented only by tiny triangular tubercles. Mesonotum unarmed.

Wing sheaths ending opposite middle of third abdominal segment. Leg sheaths ending opposite base of fifth abdominal segment, the tarsi terminating on a level or nearly so. Abdominal tergites and sternites each with four transverse rows of microscopic setae; lateral spiracles on segments 2 to 7; no apparent spiracles on dorsum of segment 8.

Dicranoptycha is a principally Holarctic genus including twelve known species, six of which occur in the United States. The flies are of medium size and of a dull, inconspicuous appearance, and are rather difficult of taxonomic separation. The life histories of members of this genus have only recently been ascertained. The following notes are taken from more detailed accounts in earlier papers by the writer (Alexander, 1919, a and b).

The habits of the immature stages of Dicranoptycha may be briefly summarized as follows: The larvae and the pupae live in rich humous soil overlain with a cover of leaf mold and other vegetable débris. They frequent open woods where there is more or less shubbery and tall herbage. Running streams or rills are not necessary for the development of the immature stages. The larvae live in the uppermost zone of the soil, where they are associated with a rather characteristic group of animal forms, such as dipterous larvae (Sciara), beetle larvae, and centipedes. They are characterized by the exceedingly long, slender body and the shiny glabrous skin, and may be confused with no other dipterous larva yet made known. The glassy appearance of the body suggests the shiny shell of a small univalve snail, the dead fragments of which occurred in some numbers in the same situations. The larvae of *Dicranoptycha winnemana* Alex., an Austral species, attain a length of from 20 to 22 millimeters, with an average diameter of only 1 millimeter. The larvae of the genus are herbivores. When ready to pupate they incase themselves in compact earthen cells, which are 10 x 3.5 millimeters in size, firm in texture, and rather thick-walled but apparently without silk. There is a small opening at either end. The pupal period is about ten days or possibly a little less. Pupation takes place in the relatively dry soil that forms the larval haunt.

The pupa of *Dicranoptycha winnemana* measures from 9.1 to 12.8 millimeters in total length. The width at the wing pad is about 1.7 millimeters. The diagnostic features are given above at some length for the genus and need not be repeated here. For other notes the reader is referred to the papers already cited.

The adult flies of the various species of Dicranoptycha are usually abundant where they occur. They may be found resting on the upper surface of leaves of shrubbery and tall herbage in open woods, often far from water, which is not so necessary for development as with most species of Tipulidae.

Subtribe **Rhamphidaria**

The division Rhamphidaria includes the genus Rhamphidia, with the possible addition of a few exotic genera. Rhamphidia is one of the constituent genera of the former group Antochini, but differs considerably from all others whose life histories have been made known. The closest relatives of Rhamphidia seem to be the Dicranoptycharia, on the one hand, and the lowermost divisions of the Hexatomini, on the other. The larvae and the pupae of Rhamphidia present a curious eriopterine appearance, but their structure indicates only a distant relationship with the Eriopterini.

Genus **Rhamphidia** Meigen (Gr. *rostrum*)

1825 *Megarhina* St. Farg. et Serv. Encyclop. Method., Ins., vol. 10, part 2, p. 585.
1825 *Helius* St. Farg. et Serv. Encyclop. Method., Index, p. 831.
1829 *Leptorhina* Steph. Cat. Brit. Ins., vol. 2, p. 243.
1830 *Rhamphidia* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 281.

Larva.— Body terete. A transverse welt, covered with microscopic scabrous points, on ventral surface of basal annuli of abdominal segments 2 to 7. Spiracular disk surrounded by five short lobes which are fringed with abundant, rather long, hairs. Head capsule massive, generalized in structure. Mandible short and stout, ending in two subequal blunt teeth. Maxilla consisting of two rather short, densely hairy lobes. Antenna short. Hypopharynx chitinized, outer margin with about a dozen teeth. Mentum not completely divided, with five teeth. Coloration of body dark brown, produced by the dense appressed pubescence covering it.

Pupa.— Cephalic crest double, the anterior part low, the posterior part the larger; lobes setiferous, divergent. Two setae on front between eyes. Pronotal breathing horns long and slender, slightly curved. Mesonotum convex. Wing sheaths reaching end of second abdominal segment. Leg sheaths ending just before posterior margin of fourth abdominal segment; all the tarsi about equal in length, or those of fore legs a little longer. Abdominal segments with two narrow basal rings and a broader posterior ring having four narrow transverse bands of spicules and comparatively few setae. Spiracles rather large on pleurites 2 to 7, and a large conspicuous pair on dorsum of segment 8.

Rhamphidia is a small genus of crane-flies (about thirty-five species), widely distributed thruout the temperate and tropical regions of the world. The larvae of the European *R. longirostris* Meig. were found by Gercke

(1884) in submerged stems of the water dock, *Rumex aquaticus* Linn. The eggs are described as being rather long, white, and granulate. It is suggested that the developmental stages may be associated with water. The two local species have been reared and are discussed herewith.

Rhamphidia mainensis Alex.

1916 *Rhamphidia mainensis* Alex. Proc. Acad. Nat. Sci. Phila., p. 498–499, fig. 14.

Rhamphidia mainensis appears to be a rather uncommon form, much rarer than *R. flavipes*, the other local species. Adult flies were not uncommon in the Basin Swamp, Orono, Maine, on June 12, 1913. This swamp is a low, sunken area surrounded on most sides by hills, opening into the " Basin," an affluent of the Penobscot River. Cold springs of water percolate down from these hillsides, and the soil is very wet, boggy, and richly filled with organic matter. The chief floral constituents are a few elms and white birches and an abundance of alders, *Spiraea latifolia* Borkh., and *S. tomentosa* Linn. The herbage consists of ferns such as Onoclea and Osmunda, patches of Iris, *Impatiens biflora* Walt., and many rushes and sedges. Crane-flies associated with *R. mainensis* on the date mentioned included the following: *Dicranomyia haeretica*, *Epiphragma fascipennis*, *Pseudolimnophila luteipennis*, *P. inornata*, *Limnophila fasciolata*, *L. macrocera*, *Pilaria recondita*, *Ulomorpha pilosella*, *Tricyphona inconstans*, *Erioptera vespertina*, and *Tipula sulphurea*, also an abundance of *Ptychoptera rufocincta* and *Bittacomorpha clavipes*.

Larvae were first found on April 20, 1917, in the dark, cold swamp known as Larch Meadows, south of Ithaca, New York. Here they occurred in the thick, black, saturated organic matter comprising the soil of the swamp. The vegetation consists of the dominant alder (*Alnus incana* [Linn.] Moench.), the poison sumac (*Rhus Vernix* Linn.), and the marsh marigold (*Caltha palustris* Linn.), as well as an abundance of other plant species in lesser numbers. The earthy material in which the crane-fly larvae were found was full of the organic remains of plants, such as ferns, leaves, alder catkins, and the like. Associated with these larvae at this time were numerous small hydrophilid beetles, and a great abundance of larvae of a dascillid beetle of the subfamily Helodinae, of various sizes and ages. Numerous tabanid and stratiomyiid larvae, and the larvae of the crane-fly species *Bittacomorpha clavipes*, *Pseudolimnophila luteipennis*, and *Tipula dejecta*, also occurred.

The larvae were conspicuous by their dark coloration and, when placed in water, by their active, snakelike movements, in this regard being very different from somewhat similar larvae of certain Eriopterini which they resemble superficially because of the five subequal lobes surrounding the spiracular disk. The indoor pupal period is six days (May 8 to 14, 1917).

Larva.— Length, 9–11.2 mm.
Diameter, 0.75–0.9 mm.

Coloration dark brown, sutures pale; pale spots on dorsum and on sides of body; spiracular disk pale, lobes marked with darker.

Form rather stout, terete (Plate XXXI, 132). Body densely covered with a long, appressed, dark pubescence. Prothoracic segment narrowed in front, long, divided into two rings by a faint constriction; mesothoracic and metathoracic segments gradually longer. First abdominal segment shorter than last thoracic segment; abdominal segments 2 to 7 long, each divided into two narrow annuli by a deep constriction which is destitute of hairs but has just before it a sharp, transverse ridge of stiff hairs; short, incomplete ridges of these stiff hairs on dorsum of anterior ring; anterior ring about half as long as posterior ring; on ventral side of each of segments 2 to 7 on anterior ring, a transverse swelling, these swellings becoming more convex and prominent on posterior segments; swellings appearing almost smooth, being covered only with microscopic, roughened points; posterior ring with a sharp ridge of hairs at about two-thirds its length. Chaetotaxy as follows: dorsal segments with short setae at about midlength of posterior ring; a single rather stout, black bristle on pleura of anterior ring, immediately above transverse swellings; a similar seta on posterior ring; two groups of very long, delicate setae on ventral face of posterior ring, one on each side of the ridge of erect hairs; thoracic segments approximately similar to abdominal segments, but sternal setae at about midlength even more prominent. Last segment of body elongated, the spiracular disk (Plate XXXI, 136) surrounded by five lobes; dorsal lobe the smallest, rather blunt, inner face with a brownish, triangular-oval mark; lateral lobes of medium length, inner face suffused with brown, which is darkest, almost black, on lower edge of lobe; ventral lobes the longest, inner face of each with two broad, parallel, blackish lines, separated by a somewhat narrower pale line; entire disk fringed around with long, dark-colored hairs, which are longest near tips of lobes, where they are strongly recurved, almost pencil-like; fringe continuous between dorsal and lateral lobes, but between ventral and lateral lobes, and between the two ventral lobes, hairs toward base of each lobe very short to lacking; ventral lobes just before tips with a single long sensory bristle. Spiracles large, subcircular, situated at base of lateral lobes, dark-colored, narrowly margined with pale. Anal gills consisting of two pairs of pale, stout, cylindrical lobes, tapering toward tips, before which there is a slight constriction.

Head capsule massive and compact, of the normal generalized limnobiine type. Labrum large, conspicuous, transverse, densely fringed with long hairs; on epipharyngeal region, a large, dense tuft of moderately elongate hairs on either side of median line. Mentum (Plate XXXI, 133) not completely divided, but with a very deep split behind, a large median tooth, and two smaller teeth on either side; behind (dorsad of) elongate median tooth, a slightly wider flattened lobe whose margins extend beyond those of outer tooth. Hypo-

pharynx a broad semicircular band of chitin whose anterior margin is provided with about a dozen teeth, the intermediate ones more blunt and rounded, the lateral teeth longer and more slender. (The antennae of this species were not distinguishable in the specimens available, but are undoubtedly similar to those of *R. flavipes* described hereinafter.) Mandible (Plate XXXI, 135) of the generalized limnobiine type, short and stout, terminating in two blunt teeth; ventral cutting edge with about three teeth which are gradually smaller toward base of mandible; a dorsal row of two teeth, of which the basal one is the smaller; base of mandible on outer face (heel) prolonged into an acute flattened blade; a conspicuous tuft of hairs at prosthecal region. Maxilla consisting of two rather short, stout lobes which are shorter than the mandible, densely provided with short hairs; palpi large, shaped like a half of a short cylinder split lengthwise.

Pupa.— Very similar to that of *R. flavipes*, as described on the following pages. (The writer has only the cast pupal skin of *R. mainensis*, and it seems to agree very closely with the pupa of *R. flavipes* except that the lobes of the labial sheaths are longer and more pointed, and the labrum is a little longer to provide for the longer rostrum of the former species.)

Nepionotype.— Ithaca, New York, April 20, 1917.
Neanotype.— Cast pupal skin, May 14, 1917.

Rhamphidia flavipes Macq.

1855 *Rhamphidia flavipes* Macq. Dipt. Exot., 5th supp., p. 17.
1856 *Rhamphidia prominens* Walk. Ins. Saunders, vol. 1, Dipt., p. 435.
1859 *Rhamphidia brevirostris* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

Rhamphidia flavipes is a common and widely distributed fly thruout the eastern United States and Canada. The species is characteristic of cat-tail swamps and similar situations. It has been reared from leaves of bur reed, Sparganium, brought in by C. H. Kennedy from Ringwood Hollow, near Etna, New York, in September. These larvae were associated with larvae of *Prionocera fuscipennis*, likewise a characteristic inhabitant of open swamps. The specimens here described were taken in a small cat-tail swamp near Bool's hillside, Ithaca, New York, in June, 1917. Here they were associated with a number of larvae of characteristic swamp-inhabiting crane-flies, such as *Ptychoptera rufocincta*, *Pseudolimnophila luteipennis*, *Limnophila macrocera*, *Pilaria recondita*, *Liogma nodicornis* (in moss), *Prionocera fuscipennis*, and *Tipula tricolor*.

This is unquestionably the larva that was found by Hart and doubtfully referred by him to the genus Erioptera (Hart, 1898 [1895]: 197–199, also Malloch, 1915–17 b: 237). Later, Mik (1898: 62) doubted that this belonged to Erioptera because of the long lashes of hairs surrounding the caudal lobes, a character not shown by typical eriopterine larvae. The larvae that Hart found were living among rushes and other vegetation floating

on the surface of the water in the Illinois River. When submerged these larvae were very active, quite as noted in the account of *R. mainensis.*

Larva.— In all general features like larva of *R. mainensis* (with the material available the writer is unable to point out differences). Present species a little larger than *R. mainensis*, measuring from 12 to 13 mm. in length and 1 mm. in diameter. Mouth parts and head capsule almost exactly like those of *R. mainensis*, already described. Antenna (Plate XXXI, 134) with first segment elongate, a little enlarged toward tip, and with an elongate, thimble-shaped papilla at tip whose surface is delicately sculptured; surrounding this papilla at tip of basal segment, a few microscopic tubercles and pegs; on face of basal segment on proximal half, a circular porous plate.

Pupa.— Length, 7.8–8.8 mm.
Width, d.-s., 1 mm.
Depth, d.-v., 1.1–1.2 mm.

Coloration light brown; abdomen paler, trivittate with dark brown; a broad, dorso-median line, and narrower, somewhat interrupted, pleural stripes; breathing horns yellow, darker at extreme bases.

Cephalic crest (Plate XXXII, 137) low, the lobes divergent, their lateral angles with a stout seta which is directed cephalad. Just behind the anterior crest a much larger, low, appressed lobe, which is transversely wrinkled, bearing on its side a seta directed dorsad. Eyes rather large, widely separated by front; two setae on front between eyes. Labrum triangular, pointed at apex. Front a little elongated to provide for short rostrum of adult. Sheaths of maxillary palpi long, stout, almost straight. Labial palpi contiguous, lying side by side at tip of labrum. Antennae rather widely separated at their bases, ending just beyond wing root; in malec lying across face of eye, due to the large size of eyes in this sex.

Mesonotum prominent, carinate medially (Plate XXXIII, 142). Breathing horns long and slender, slightly curved, transversely crenulated, a little enlarged toward tips; proximo-cephalad of base of each horn a small rounded tubercle bearing two setae. Lateral angles of thorax with about three short setae. Mesonotum convex, transversely wrinkled, with a few very short setae. Wing sheaths ending about opposite posterior margin of second abdominal segment. Leg sheaths parallel, about subequal in length or those of fore legs a little longer, ending just before posterior margin of fourth abdominal segment. Dorsal abdominal segments (Plate XXXIII, 143) each with two narrow basal rings and a much broader posterior ring; ventral segments (Plate XXXIII, 144) with the two basal rings confluent; dorsal segments with each narrow basal ring having a narrow, slightly arcuated band of spicules, and posterior ring having a narrow basal band of spicules which is more or less arcuated, and a straight caudal band, immediately in front of which are four groups of two setae each, or, in some specimens, with the intermediate groups reduced to a single seta; ventral segments with posterior ring having a broad transverse band of spicules, with three setae in alinement at each end of this band; closer to base of segment, two strong setae on either side; anterior ring darkened. Pleura with large but apparently nonfunctional spiracles on segments 2 to 7, a strong ante-spiracular seta, and three post-spiracular setae, as illustrated (Plate XXXIII, 144). Male cauda (Plate XXXII, 139 and 140) terminating in two acute tips which are directed dorsad; at base of these lobes on

dorsal face, two blunt, approximated, parallel lobes directed cephalad; at the base of long apical lobes, a shorter, pointed, setiferous lobe, directed laterad and dorsad, bearing on its side and near the apex a few setae. Dorsum of segment 8 with four prominent lobes surrounding a hollow, these lobes ending in acute tips, the posterior pair directed more dorsad, the anterior pair directed more laterad, at the base of the latter a pair of spiracles. Female cauda similar but with acidothecae prolonged, bearing on the side prominent lateral lobes (Plate XXXII, 141), corresponding to the setiferous lobe of male as described above; quadrangle of tubercles on dorsum of segment 8 (Plate XXXII, 138) about as in male, all the tubercles ending in chitinized points.

Nepionotype.— Ithaca, New York, May 11, 1917.
Neanotype.— Ithaca, New York, June 3, 1917.
Paratypes.— Pupae with neanotype.

Tribe **Hexatomini**

The tribe Hexatomini, as here understood, comprises a very extensive group of medium-sized crane-flies, made up of the members of the former groups Limnophilini and Hexatomini. The more generalized members of the group are herbivorous, but the two highest subtribes, Limnophilaria and Hexatomaria, are carnivorous in their feeding habits.

The larvae of the lower divisions have the head capsule massive and compact, the mentum chitinized and with the anterior margin toothed, and the hypopharynx usually well preserved. The mandibles are not formed into long, curved hooks, and the maxillae are of a generalized organization. The higher subtribes, Limnophilaria and Hexatomaria, have the head capsule long and slender and very much dissected, with the constituent plates very narrow and separate. The mentum is very reduced or lacking, in some of the Limnophilaria consisting of an articulated transverse bar which is grooved with parallel fine striae. In the group Ulomorphae and in the Hexatomaria the chitinized mental region is nearly, if not quite, lacking, allowing for great distention of this region of the head. The mandibles are powerful, curved hooks, bearing a few teeth at about midlength. In the group Ulomorphae the mandibles are hinged at about midlength, the basal part being deeply grooved on the inner face to receive the blade in a position of rest. The maxillae have the outer lobe prolonged into an elongate flattened blade which extends out of the thoracic orifice when the head is retracted.

The pupae of the Ularia and the Epiphragmaria have a pair of large spiracles on the dorsum of the eighth abdominal segment, indicating a close phylogenetic relationship with the Limnobiini. Dactylolabis has

the lateral abdominal spiracles protuberant, with those of the second segment very large and conspicuous. Pseudolimnophila, the Ulomorphae, and Pilaria have the pronotal breathing horns very long and slender, with the tips split into divergent flaps. In the Hexatomaria the lateral abdominal spiracles are large and functional.

The immature stages of the Polymeraria, including the single tropical American genus Polymera Wiedemann, are unknown. Their discovery might result in the inclusion of this subtribe with the Pediciini rather than with the Hexatomini.

The following keys separate the subtribes of the tribe Hexatomini:

Larvae

1. Mentum completely divided, each half with seven teeth on anterior margin; hypopharynx a semicircular chitinized ring with numerous teeth around anterior margin. *Pseudolimnophilaria* (p. 848)
   Mentum when present not divided; hypopharynx not shaped as above 2
2. Abdominal segments 2 to 7 with a basal transverse creeping-welt 3
   Abdominal segments 2 to 7 without such a welt 4
3. Mentum three-toothed; antenna elongate, the apical segment hemispherical. *Epiphragmaria* (p. 843)
   Mentum nine-toothed; antenna short, subglobular, the apex with two short papillae. *Ularia* (p. 838)
4. Body depressed; head capsule massive, compact; mentum heavily chitinized, seven-toothed; maxilla not projecting .... *Dactylolabaria* (p. 852)
   Body terete; head capsule of slender bars, not compact; mentum feeble, at most a narrow, transverse bar which is delicately striate; maxilla projecting from thoracic orifice 5
5. Mental bar present .... *Limnophilaria* (group *Limnophilae*) (p. 858)
   Mental bar lacking 6
6. Dorsal plates of head capsule firmly united; epipharynx and maxilla densely hairy; mandible hinged .... *Limnophilaria* (group *Ulomorphae*) (p. 869)
   Dorsal plates of head capsule widely separated, at most merely contiguous behind; epipharynx and maxilla not hairy; mandible not hinged .... *Hexatomaria* (p. 876)

Pupae

1. Two large spiracles on dorsum of eighth abdominal segment 2
   No large spiracles as above 3
2. Pronotal breathing horns subchitinized, directed strongly ventrad; abdominal segments without shagreened transverse bands; pupates in wood .... *Epiphragmaria* (p. 843)
   Pronotal breathing horns flattened, directed laterad; shagreened transverse bands on abdominal segments; pupates in earth .... *Ularia* (p. 838)
3. Abdominal segments with large protuberant spiracles, those on second segment very large .... *Dactylolabaria* (p. 852)
   Abdominal segments without conspicuous protuberant spiracles 4
4. Pronotal breathing horns elongate, split into two flaps at tip 5
   Pronotal breathing horns not split into two such flaps 6
5. Abdominal segments with five or six rows of setiferous tubercles. *Pseudolimnophilaria* (p. 848)
   Abdominal segments without such rows of tubercles. *Limnophilaria* (group *Ulomorphae*) (p. 869)

6. Head and thorax without spines or tubercles; lateral abdominal spiracles small. *Limnophilaria* (group *Limnophilae*) (p. 858)
   Head and thorax often with tubercles on antennal scape, labrum, or mesonotal scutellum; lateral abdominal spiracles large, functional.................... *Hexatomaria* (p. 876)

The most important literature on the tribe Hexatomini is as follows:

Ula macroptera	Larva	Stannius, 1829:205.
Ula macroptera	Larva, pupa, general	Perris, 1849:337–341.
Ula macroptera	General	Alexander, 1915 a:2.
Ula macroptera	General	Pierre, 1919–20:76.
Ula bolitophila	General	Loew, 1869:4–5.
Ula elegans	Larva, pupa, general	Alexander, 1915 a.
Ula elegans	Larva, pupa	Malloch, 1915–17 b:226. (Copy.)
Epiphragma picta	Larva	Bremi-Wolf, 1846.
Epiphragma picta	Larva, pupa	Beling, 1873 b:589–590.
Epiphragma fascipennis	Larva, pupa, general	Needham, 1903:281–285.
Epiphragma fascipennis	Larva, pupa	Malloch, 1915–17 b:224–225. (Copy.)
Pseudolimnophila luteipennis	Larva, pupa, general	Hart, 1898 [1895]:202–204.
Pseudolimnophila luteipennis	Larva, pupa, general	Malloch, 1915–17 b:222–223.
Dactylolabis wodzickii	Larva, pupa, general	Nowicki, 1867:340–343.
Dactylolabis denticulata	Larva, pupa, general	Mik, 1894.
Limnophila ferruginea	Larva, pupa, general	De Meijere, 1916:204–206.
Limnophila hyalipennis	Larva, pupa	Beling, 1886:198–199.
Limnophila lineola	Pupa	Beling, 1879:54.
Limnophila lineola	Larva	Beling, 1886:199–200.
Limnophila nemoralis	Larva, pupa	Beling, 1886:200–201.
Limnophila ochracea	General	Beling, 1886:202.
Limnophila pallida	Larva, pupa	Beling, 1873 a:556–558.
Limnophila dispar	Larva, general	Perris, 1849:331.
Limnophila pictipennis	Larva, pupa, general	Beling, 1879:51–52.
Limnophila pictipennis	Larva	Brauer, 1883:55.
Limnophila punctata	Larva	Scheffer, in Rossi, 1848:10.
Limnophila punctata	Larva	Osten Sacken, 1869:201.
Limnophila punctata	Larva, pupa, general	Beling, 1886:195–197.
Limnophila punctata	Larva	Gerbig, 1913:158–161.
Limnophila punctata	General	Cameron, 1917:63.
Limnophila bryobia	General	Mik, 1881:205–206.
Limnophila sinistra	Larva, pupa	Hudson, 1920:33–34.
Pilaria fuscipennis	Larva, pupa	Beling, 1886:197–198.
Pilaria fuscipennis	Larva	Gerbig, 1913:164–166.
Pilaria fuscipennis	General	Cameron, 1917:63.
Pilaria discicollis	Larva	Gerbig, 1913:163–164.
Pilaria discicollis	General	Cameron, 1917:63.
Pilaria tenuipes	Pupa	Hart, 1898 [1895]:204–205.
Pilaria tenuipes	Pupa	Malloch, 1915–17 b:223–224.
Eriocera spinosa	Larva, pupa, general	Alexander and Lloyd, 1914:27–30.
Eriocera spinosa	General	Alexander, 1915 c:149.
Eriocera cinerea	Larva	Alexander and Lloyd, 1914:21–23 (as *longicornis*).
Eriocera longicornis	Pupa, general	Alexander and Lloyd, 1914:23–27.

Eriocera longicornis	General	Alexander, 1915c: 149–152.
Eriocera fultonensis	Larva, pupa, general	Alexander and Lloyd, 1914: 30–33.
Hexatoma nigra	General	Von Röser, 1834.
Hexatoma megacera	Larva, pupa, general	Alexander, 1915c: 141–148.
Penthoptera albitarsis	Larva, pupa, general	Alexander, 1915c: 152–157.

Subtribe Ularia

The division Ularia includes only the genus Ula. It represents a very primitive group of crane-flies, presumably the most generalized of the entire tribe. The head capsule of the larva is oval and very massive, with the prefrons large and distinct. The head capsule and its arrangement of setae is not conspicuously unlike that of the eucephalous families of crane-flies, and this group of Tipulidae is presumably not very different from the early tipulid ancestors. The mentum is heavily chitinized, not completely divided behind, consisting of two plates, one behind the other. The outermost plate terminates in three teeth, while the second plate furnishes three additional teeth on each side. The hypopharynx is not chitinized. The antennae are very small; the basal segment is nearly globular, bearing at its tip two blunt, conical papillae. The mandibles are slender; the ventral cutting edge has about five narrow teeth; there is a distinct brush of hairs at the prostheeal region. The maxillae are of a generalized type, with the palpus large, flattened, and disklike. The abdomen is provided with six creeping-welts on the ventral surface of the segments. The spiracular disk is moderate in size, squarely truncated, surrounded by five subequal lobes which are heavily marked with black on their inner faces.

The pupa has the cephalic crest small and provided only with very small setae. The pronotal breathing horns are very long, tapering to the subacute tips. The abdominal segments have a basal transverse band of a shagreened appearance. The dorsal spiracles on the eighth abdominal segment are large and distinct.

The closest relative of the division is apparently the genus Epiphragma in the subtribe Epiphragmaria. But this entire group of genera (those included in the subtribes Ularia, Epiphragmaria, and Pseudolimnophilaria) is not far removed from the tribe Limnobiini.

Genus Ula Haliday (Gr. *soft*)

1833 *Ula* Hal. Ent. Mag., vol. 1, p. 153.
1864 *Macroptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 224.

Larva.— Body covered with a short pubescence. Basal annuli of abdominal segments 2 to 7 with a transverse creeping-welt on ventral surface. Spiracular disk squarely truncated, surrounded by five subequal lobes which are fringed with very short hairs. Head capsule massive, prefrontal sclerite very large, tapering to a point behind. Labrum large, conspicuous, with tufts of hairs. Mandible slender; ventral cutting edge with five teeth; a tuft of hairs on prosthecal region. Maxilla simple; palpus large. Antenna very small; basal segment subglobular, with two apical sensory papillae. Mentum not deeply divided behind; outer plate with three apical teeth; inner plate adding three additional teeth to each side. Hypopharynx not chitinized.

Pupa.— Cephalic crest small, setae tiny. Pronotal breathing horns long, tapering to subacute, flattened apices. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths ending at about midlength of sixth abdominal segment. Abdominal segments on tergites and on apical sternites with transverse bands of microscopic points, producing a shagreened appearance; dorsal spiracles on segment 8 conspicuous.

The genus Ula includes only six described species, of which three are European, two are North American, and one is Javanese.

The adult flies of the American species are commonest in spring and late summer. They frequent cool, shaded gorges and ravines, or dark woods in mountainous regions, and may be swept from beds of low vegetation, such as ferns, yew, and other species.

The larvae of all the known species live in various species of fungi, but go to earth for pupation.

In Europe the common genotype, *Ula macroptera* (Macq.), has been discussed rather frequently in the literature. Stannius (1829:205) found the larvae in a species of Agaricus. Perris (1849:337–341) furnishes a brief account of the species, from which the following notes are taken: The fungus in which the larvae were found was *Hydnum erinaceum* Bull., growing on the trunks of living oak trees. The larvae are gregarious and frequent galleries in the fungus, along which they progress by means of their mandibles, by their ambulatory feet, and by the short hairs that cover the body. They were found in the month of November. A month later they went into the earth, where they transformed as pupae. The pupae bear a strong resemblance to those of Limnophila, but differ in the shape of the pronotal breathing horns. In February and March the pupae come to the surface of the earth and the adults emerge. The

caudal end of the larva is described as having but four lobes; no mention is made of the median dorsal lobe found in the American species, and it is presumably lacking or very reduced in size. Pierre (1919–20:76) has reared this species from larvae living in *Russula nigricans* Fries.

Another European species, *U. bolitophila* Loew, was bred from larvae living in fungi on beech trees in Austria (Loew, 1869:4–5).

In America, the immature stages of *Ula elegans* have been discussed by the writer (Alexander, 1915a), the notes given below being in part supplementary to his earlier account.

Ula elegans O. S.

1869 *Ula elegans* O. S. Mon. Dipt. N. Amer., part 4, p. 276–277.

Ula elegans is a rather common species in mountainous regions thruout the northeastern United States. The adult flies swarm in early spring and again in the fall. At Ithaca, New York, on May 14, 1912, the writer found them swarming at half past four in the afternoon. There were about fifteen to twenty individuals in a swarm within a foot or two of the ground. In some cases the swarms were reduced to two or three individuals, or in a few instances to a single specimen. In copulation the flies rest on the upper surface of near-by plants (Symplocarpus, in the instance cited), with all the legs on the support. Copulation is rather firm, and the insects fly for short distances still united. The only crane-fly associated with Ula at that time was *Limnophila ultima* O. S.

On September 15, 1912, the writer found a fleshy species of fungus (Fomes) growing on a much-decayed stump close to the ground. This fungus contained a number of crane-fly larvae, including about thirty-five larvae of *Limnobia cinctipes*, a lesser number of *L. triocellata*, and many larvae of *Ula elegans*. The larvae of these species frequented the upper layers of the mushroom and had reduced the surface to a semi-liquid state. At the end of a week the whole fungus was reduced to a very decayed condition. The fungus, which was taken at Gloversville, New York, was then transferred to Ithaca, and was placed in large glass jars, with sand in the bottom to take up the liquids produced by decay and to provide a place for pupation. The first adults emerged on October 14. Emergence continued until the 27th, when the remaining pupae were killed and placed in alcohol. At that time they were very dark-

colored and evidently nearly ready to emerge to the adult state. At times the larval movements are very active and eel-like, but at other times they are very slow and sluggish. At each movement forward, the terminal segment partly telescopes into the subterminal and is thrown violently backward. After transforming to the adult condition, the pupal skin is left adhering to the sand, with the posterior half, or a smaller portion, attached, often standing quite perpendicular to the surface and very conspicuous.

Larva.— Length, 8.5–11.9 mm.
Diameter, 1.4–1.8 mm.

Color dull white; head capsule very dark brownish black.

Form moderately slender (Plate XXXIV, 145), but the body not greatly elongated as in the Eriopterini and some Limnobiini. Integument covered with a fine, short pubescence. Abdominal segments 2 to 7 each divided by a constriction into a narrow basal annulus and a broad posterior annulus; basal ring at about midlength and at the end with narrow transverse rows of tiny setae; abdominal segments 2 to 7 on ventral surface of basal ring with conspicuous raised transverse creeping-welts which are covered with microscopic points; eighth abdominal segment suddenly constricted before spiracular disk. Region around anus protuberant, this evidently being an aid to propulsion. Spiracular disk (Plate XXXIV, 153) surrounded by five blunt lobes, of which the dorsal one is median in position and blunter than the others; inner face of each lobe with a conspicuous brownish black mark; a fringe of delicate blackish hairs surrounding disk, these hairs a little longer and more prominent at ends of lobes. Spiracles almost circular, widely separated, the distance between them being about three times diameter of one spiracle. Disk between spiracles with an indistinct arcuated line.

Head capsule (Plate XXXIV, 146) massive and compact, rather narrow, posterior incisions not extending deeply into capsule. Prefrons very large, tapering gradually to a sharp point behind; numerous setae on prefrons and on other sclerites of capsule. Labrum (Plate XXXIV, 147) large, conspicuous; epipharynx and lateral margins strengthened by narrow bands of chitin; lateral and anterior margins of labrum with a dense fringe of long hairs; an irregular tubercle on dorsal surface on either side of labrum; epipharynx with a narrow transverse band of setae; juncture of clypeus and labrum with four setiferous punctures, two on either side, the posterior pair a little the closer together; clypeal region with a dark transverse basal and terminal band; base of clypeus with three setiferous punctures on either side. Mentum (Plate XXXIV, 148) almost completely undivided, the usual median split obliterated except behind; outermost mental plate terminating in three apical teeth, the median one of which is a little shorter and broader than the other two; behind (dorsad of) outer plate, another similar plate which adds three more teeth to each side of mentum. Hypopharynx not chitinized. Antenna (Plate XXXIV, 149) very small, short, cylindrical or subglobular, about as broad as long; at the tip two hyaline papillae shaped like immature mushrooms, the outer one about twice the size of the inner one. Mandible (Plate XXXIV, 150 and 151) slender, ending in a blunt, slightly curved, apical point; on ventral cutting edge a row of about five flattened

teeth; the more apical ones larger, the basal one very broad and truncated; two or three dorsal teeth, gradually lessening in size from tip of mandible toward base; two conspicuous tufts of long setae at prostheeal region; base of mandible on dorsal side with a large, somewhat curved, plate overlying head sclerites. Maxilla (Plate XXXIV, 152) with cardo long and narrow, transverse, with three conspicuous setiferous punctures bearing long setae; outer lobe short and stout, a little narrowed to tip; palpus rather large, flattened, disklike, the truncated apex with several tiny hyaline pegs; inner lobe with a sensory bristle and an inner fringe of rather short hairs.

Pupa.— Length, 6.4–7 mm.
Width, d.-s., 1.2–1.3 mm.
Depth, d.-v., 1.2–1.6 mm.

Mouth parts, wing sheaths, and leg sheaths rather dark brown; thoracic dorsum and abdomen light yellowish brown; pronotal breathing horns dark brown, passing into light yellow on apical third or quarter; mesonotal prescutum retaining its light color even in old pupae and those preserved in alcohol.

Cephalic crest (Plate XXXV, 155) represented only by a small bilobed protuberance behind and between antennal bases, each lobe tipped with a very tiny seta. Labrum short, bluntly rounded at tip. Labial lobes appearing as a large, roughly quadrate plate, a little narrowed behind and with all angles rounded. Sheaths of maxillary palpi very long and slender, rather stout at base, tapering to blunt tip. Antennae not conspicuous, rather widely separated at bases, ending just before or opposite origin of wing pad.

Pronotal breathing horns (Plate XXXV, 154 and 155) long and conspicuous, cylindrical, gradually tapering to subacute and flattened apices; horns directed laterad and cephalad, widely divergent. Thoracic dorsum without lobes or spines. Wing sheaths extending to just beyond end of second abdominal segment. Leg sheaths extending to about midlength of sixth abdominal segment; tarsal sheaths ending almost on a common level, the fore legs being a very little the longest, the middle legs a little shorter. Abdominal tergites with transverse rows of scattered punctures; on tergites 2 to 6 a transverse band of subchitinized points, producing a shagreened appearance; these bands located on basal rings of segments excepting the last two, which are on extreme ends of segments 5 and 6; on sternites the bands appearing only on segments 7 and 8, the other sternites being largely concealed by the unusually long leg sheaths; band on segment 8 very broad, but narrowly interrupted medially. Male cauda with ventral lobes bluntly rounded and inclosing pleural appendages of adult (in fully colored pupae these show thru the pupal skin as from twelve to fifteen strong, chitinized points on the inner posterior face); dorsal lobes (Plate XXXV, 157) very short and blunt, and closely approximated medially; on eighth tergite a broad rectangle of five lobes, including an anterior and a posterior lobe on either side and a much broader anterior median lobe; just proximad of anterior lateral lobes a large and distinct spiracle, in the cast skin with the large tracheal trunks still attached. Female cauda (Plate XXXV, 156) stout, tergal valves a little longer than sternal valves and a little upcurved.

Nepionotype.— Ithaca, New York, October 14, 1912.
Neanotype.— With type larva.
Paratypes.— Type locality, October 12 to 19, 1912.

Subtribe **Epiphragmaria**

So far as is known to the writer, the division Epiphragmaria includes only the genus Epiphragma. The immature stages are of a very primitive organization. The larvae have the head capsule broad and massive, with the posterior incisions very shallow. The labrum is broad, with lateral tufts of hair. The mentum is heavily chitinized, entire, with only a single lateral tooth on either side of the median tooth. The hypopharynx is not chitinized but the entire surface is provided with rows of tiny spinous points, somewhat as in the Dicranoptycharia. The antennae have the terminal papillae hemispherical. The mandibles are not greatly elongated; each has an apical tooth and two rows of lateral teeth. The maxillae are very simple in structure. The abdomen is provided with six ventral creeping-welts. The spiracular disk is large and simple, with the lobes short and obtuse.

The pupa has the breathing horns heavily chitinized, tapering to acute, slender points. The spiracles on the dorsum of the eighth abdominal segment are large and conspicuous.

The relationships of this group are obviously with the Rhamphidaria of the Limnobiini and the Ularia of the Hexatomini, the three groups probably being closer together phylogenetically than their arrangement in tribes would indicate. From a study of the adults alone, there seems to be little connection between the genera Rhamphidia, Epiphragma, and Ula, which were placed in three widely separated tribes by Osten Sacken. A study of the immature stages, the structure of the larval head, the abdominal creeping-welts, and the dorsal spiracles of the eighth abdominal segment of the pupa, indicate a relationship that cannot be denied.

Genus **Epiphragma** Osten Sacken (Gr. *upon + partition*)

1859 *Epiphragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Larva.— Body nearly smooth; basal annuli of abdominal segments 2 to 7 with a naked transverse creeping-welt on ventral surface. Spiracular disk large, with four or five lobes, the dorso-median lobe often reduced. Spiracles large, circular. Anal gills four, retractile. Head capsule massive. Labrum broad, with lateral tufts of hairs and with two setae on anterior margin. Mandible with a blunt apical tooth and two rows of two lateral teeth. Maxilla small, simple; palpus large; inner lobe with a dense tuft of stiff hairs. Antenna two-segmented; basal segment elongate, apical papilla hemispherical. Hypopharynx not chitinized. Mentum entire, with only three teeth — a slender median tooth, and a broad, flat tooth on either side.

Pupa.— Cephalic crest erect, rectangular, the outer lateral angles produced into strong, chitinized spines. Pronotal breathing horns large at base, the elongate tips nearly chitinized, tapering into subacute points. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths terminating just before end of fifth abdominal segment. Abdominal tergites with a transverse band of spicules at caudal margin; pleurites with a transverse oval area of similar spines; terminal sternites with a similar transverse band of spicules, most powerfully developed on segment 8; dorsal spiracles on segment 8 conspicuous.

Epiphragma is a rather small genus (twenty-five species) of usually large and handsome crane-flies, finding its center of distribution in the tropical regions of the New World. The adult flies of the local species are usually common. *Epiphragma fascipennis*, the best known of these species, is often found swarming in shady places, the swarms usually consisting of from twelve to fifteen individuals.

The immature stages of all the species thus far known are spent in decaying wood. In Europe, Beling (1873 b: 589–590) records finding larvae and pupae of *E. picta* (Fabr.) in decaying ash (Fraxinus) and beech (Fagus) in the spring. He gives the pupal duration of this species as about two weeks. Needham (1903: 281–285) gives an excellent account of *E. fascipennis*, which he found in partly decayed stems of willow and button-bush. The same species has been found living in the stems of black ash and elm. *E. solatrix* has been found in various deciduous trees in a dead or decaying condition. Bruch (*in litt.*) records an Argentinian Epiphragma from decaying wood.

Epiphragma solatrix (O. S.)

1859 *Limnophila* (*Epiphragma*) *solatrix* O. S. Proc. Acad. Nat. Sci. Phila., p. 238.

Epiphragma solatrix is a beautiful crane-fly, a little more Austral in its distribution than the more widely distributed *E. fascipennis*. H. S. Barber found larvae and young pupae very numerous in a drift log of sycamore (Platanus) at Plummers Island, Maryland, on May 19, 1913, and it is the study of this material that is included in this paper. Shannon found larvae in rotten wood at Rosslyn, Virginia, on November 23 and 25, 1912, and a pupa on January 3, 1913. Later he reared both *E. solatrix* and *E. fascipennis* from larvae taken from the same log on the same day. The species was again found in a decaying maple log on the Potomac River opposite Plummers Island, Maryland, where it was associ-

ated with the larvae of the syrphid fly, *Temnostoma bombylans* (Fabr.) and the supposed larva of Protoplasa (p. 770).

Larva.— Length, 18 mm.
Diameter, 1.6 mm.

Coloration pale whitish; anterior segments of body brighter-colored, more reddish.

Form stout and plump, not narrowed at ends of body. Pronotum longer than other thoracic segments. Integument covered with a short appressed pubescence. Abdominal segments 2 to 7 with conspicuous white creeping-welts on ventral surface of basal ring; these welts not interrupted medially, and entirely naked. Spiracular disk (Plate XXXVI, 163) large, unmarked, surrounded by five short lobes, the ventral pair very widely separated; dorsal lobe broad and obtuse; entire disk fringed with very short, delicate hairs which are interrupted only between paired lobes; inner face of lobes suffused with pale brown at tips. Spiracles large, circular, reddish with a very broad yellow margin, separated by a distance nearly equal to two times the diameter of one spiracle. Anal gills four, retractile.

Head capsule (Plate XXXVI, 158) broad and massive, the constituent plates firmly united except on ventral parts. Labrum broadly transverse; a median epipharyngeal part whose surface is finely pitted, bearing on ventral side near margin two stout setae; lateral angles of labrum directed proximad and densely tufted with hairs; extreme lateral margins of labrum with a curved hyaline seta; juncture of labrum and clypeus with two large setiferous punctures on either side; a few setiferous punctures on head capsule. Mentum (Plate XXXVI, 159) heavily chitinized, the outer face terminating in a single median tooth, behind which is a tridentate plate with three flattened teeth, the lateral ones very broad. Prementum (Plate XXXVI, 160) lying just behind mentum, a moderately broad transverse plate whose anterior margin is deeply and almost squarely notched, the lateral lobes thus formed being rounded or feebly indented at their tips. Hypopharynx (Plate XXXVI, 161) lying above and connected with prementum, consisting of a large flattened lobe, whose outer margin is evenly rounded, the surface densely set with longitudinal rows of small, subacute papillae. Antenna short, two-segmented; basal segment cylindrical, with auditory plate almost basal in position; apical segment small, subglobular or hemispherical. Mandible moderate in size, broad at base with a blunt apical tooth and a few blunt lateral teeth, two on dorsal cutting edge and two on ventral cutting edge, the more basal of these latter tending to be evanescent; two stiff setae at heel of mandible; a triangular lobe on dorsal face which projects onto lateral parts of labrum. Maxilla (Plate XXXVI, 162) primitive in structure; cardo elongate, transverse, with four setiferous punctures bearing powerful setae; outer lobe glabrous, with palpus at its tip; palpus slightly elongate, the auditory plate just before midlength; a seta on outer lobe below palpus; inner lobe of maxilla with a dense terminal brush of stiff yellow hairs and a few sensory papillae.

Pupa.— Length, 12–12.5 mm.
Width, d.-s., 2–2.1 mm.
Depth, d.-v., 2–2.1 mm.

Head, thorax, and appendages brown, becoming darker with age; pronotal breathing horns light red; abdomen whitish, the terminal rows of spicules on the segments chitinized.

(In older specimens the wing pattern shows on the sheath and is not distinctly fasciate as in *E. fascipennis.*)

Cephalic crest (Plate XXXVII, 166) erect, rectangular, the outer lateral angles directed ventrad and laterad as powerful chitinized spines, which in most cases curve outward; a stout seta beneath each spine. Labrum subtruncated or indistinctly bilobed at apex. Labial lobes triangular, projecting caudad as two cones. Maxillary palpi bent backward, lying along margin of cheek, stout, tapering suddenly to blunt tips. Cheeks projecting as flattened ledges. Antennae moderate in length, on scapal segment with a flattened tubercle on either side of cephalic crest; antennae extending rather far beyond wing root.

Pronotal breathing horns (Plate XXXVII, 164) with base enlarged, the elongate, subchitinized tips gradually narrowed, and the extreme apices subacute; breathing horns at tips directed ventrad and proximad; a truncated setiferous tubercle before each breathing horn. Mesonotum very deep. A short, but high, median crest behind breathing horns. Lateral angles of thorax produced into a slender lobe bearing a stout seta at tip. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths terminating just before end of fifth abdominal segment; middle tarsal sheaths usually a little shorter than the others; in some specimens, especially females, fore legs the shortest, hind legs the longest. Abdominal segments (Plate XXXVII, 167) with two narrow basal rings and a broader posterior ring. Tergites on segments 2 to 7 near caudal margin of posterior ring with a narrow transverse crossband densely beset with acute spicules; on posterior segments these bands becoming gradually weaker, on segment 7 being very weak; two setae near lateral margin of posterior ring at about midlength. Pleurites with a transverse oval area with about twenty sharp spines near caudal margins of segments; a stout seta lying cephalad of this area. Spiracles distinct, oval, lying on ventral cephalic part of pleural posterior ring; a seta near dorsal margin of second basal ring. Sternites with a transverse band of spicules on segments 5 to 8, these being weakest on segment 5 at ends of tarsal sheaths and very strong and powerful on segment 8, where the band is interrupted medially; band often rather narrow but sometimes much broader. A seta near midlength of posterior ring on either side. Male cauda (Plate XXXVIII, 170) with dorsal lobes very stout, globose at base but soon narrowed into slender cylindrical appendages, each bearing three setae at tip; viewed from above, these lobes are seen to be separated by a wide U-shaped notch; ventral lobes blunt and with a flattened depressed disk at base of incision; eighth segment with a wide rectangle of lobes, two posterior lobes that are weakly setiferous and two smaller anterior lobes with a large spiracle proximad of each. Female cauda (Plate XXXVIII, 171) with tergal valves a little longer than sternal valves, upcurved, and with a stout seta before tip.

Nepionotype.— Plummers Island, Maryland, May 19, 1913.
Neanotype.— With type.
Paratypes.— Larvae and pupae with type.

Epiphragma fascipennis (Say)

1823 *Limnobia fascipennis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 19.
1859 *Limnophila (Epiphragma) pavonina* O. S. Proc. Acad. Nat. Sci. Phila., p. 239.
1869 *Epiphragma fascipennis* O. S. Mon. Dipt. N. Amer., part 4, p. 194.

Epiphragma fascipennis is a very common crane-fly thruout eastern North America. As already stated, the immature stages are spent in decaying or partly sound wood, a wide variety of deciduous trees and shrubs being chosen, such as willow, elm, ash, buttonbush, and others. Needham gives the pupal duration as about twelve days, larvae and pupae found on May 18 emerging as adults on the 30th. A fully grown larva that the writer found in a decayed log beneath moss at Ithaca, New York, on May 8, 1917, pupated early in the morning of the 10th. The specimen died on the 18th, when about to emerge, and this would give a much shorter pupal period than is generally recorded for the genus. It was noted at the same time that the larva superficially resembles the larva of the leptid fly *Chrysopila thoracica* (Fabr.), with which it was associated but from which it is easily distinguished by its massive head capsule.

Needham found abundant pupae in a decaying log of black ash (Fraxinus) near Freeville, New York, on May 6, 1915. The pupae occurred in burrows in the semi-decayed wood. Adults emerged on the 11th. Additional material was found at Mud Creek, near Freeville, on May 15, 1915, in elm (Ulmus).

The account of the habits of the larvae as observed in Illinois by Needham (1903:281–285) is here quoted in part:

> The larvae bore in the dead and fallen stems of buttonbush and willow, where these lie on the mud at the borders of shallow ponds. I found them always in stems that were still partially sound, tunneling beneath the bark or even into the deeper parts and into the sounder wood. These stems are frequently submerged in spring and autumn, and even in summer, when the pond has gone dry, they are always saturated with moisture. . . . .
>
> The most interesting thing about the larva, aside from its wood-boring habits, is its singular adaptation to amphibian life. It must needs live part of the time wholly submerged beneath the waters of the pond, and part of the time out on land; it has, therefore, both open spiracles and tracheal gills; and, moreover, its tracheal gills are so placed that they may be withdrawn into the body in a dry time, where they escape the ills of too rapid evaporation.

In his description of the immature stages, Needham points out a probable error of Beling in describing a sexual dimorphism in the larvae of a species of this genus — Beling stating that the larvae producing females have three caudal lobes while those producing males have five. Malloch (1915–17b:224–225) cites Needham's descriptions of this species.

Larva.— (No larvae are available to the writer for a comparison with this stage of *Epiphragma solatrix*, but from Needham's characterization, and manuscript notes on specimens taken at Ithaca, New York, by the writer, the following differences seem to hold):

Spiracular disk surrounded by but four lobes, the dorso-median lobe being very reduced; inner faces of these lobes, as well as disk itself, entirely unmarked with darker.

Pupa.— Similar to pupa of *Epiphragma solatrix*, but differing as follows:

Cephalic crest (Plate XXXVII, 165) low, the lateral horns shorter, not elevated, and directed ventrad or slightly downward; setae on lateral face of spines often projecting above (cephalad of) it. Pronotal breathing horns shorter and stouter than in *solatrix*. Spines on eighth abdominal sternite widely separated or interrupted on median line. Male cauda (Plate XXXVIII, 169) with dorsal lobes much stouter than in *solatrix*.

Neanotype.— Bool's hillside, Ithaca, New York, May 8, 1917.
Paratype.— Pupa, Mud Creek, Freeville, New York, May 15, 1915.

The type pupa has one of the pronotal breathing horns deformed and bent caudad so as to be appressed against the body. Needham, who has a very much larger series available for study, notes this same peculiarity when he states that "a crumpled horn on one side is of rather common occurrence" (Needham, 1903:284).

Subtribe **Pseudolimnophilaria**

As at present constituted, the division Pseudolimnophilaria includes the single genus Pseudolimnophila, but other groups may be added to it when the immature stages of other species of the old genus Limnophila are made known. The larva is of a distinctly primitive type, the head capsule being compact and massive, the mentum chitinized and completely divided, each half provided with seven or eight teeth. The hypopharynx is a heavily chitinized semicircle with numerous teeth around the anterior margin. The antennae bear two elongate apical papillae. The mandibles each have two blunt apical teeth and two rows of lateral teeth.

The pupa is similar to that of the Limnophilaria, but the abdominal segments have transverse rows of setiferous tubercles.

The larva shows many points of resemblance to the tribe Limnobiini, and the two groups are probably derivable from an immediate common ancestor.

Genus **Pseudolimnophila** Alexander (Gr. *false* + *Limnophila*)

1919 *Pseudolimnophila* Alex. Cornell Univ. Agr. Exp. Sta., Mem. 25, p. 917.

Larva.— Body covered with delicate appressed hairs and numerous erect setae. Spiracular disk surrounded by four lobes, the ventral pair very long and narrow, with long fringes of hair. Gills four, long and slender. Head capsule massive, the sclerites large, fused.

Mandible short and blunt, of the generalized limnobiine type, the two apical teeth blunt. Maxilla not greatly projecting. Antenna slender, with two elongate apical papillae. Hypopharynx a chitinized band, with numerous teeth along anterior margin. Mentum completely divided, each half with about seven teeth.

Pupa.— Cephalic crest tipped with long setae. Pronotal breathing horns elongate, tips deeply split into divergent flaps. Abdominal segments with transverse rows of setiferous tubercles, there being five such rows on the tergites and six on the sternites. Lateral spiracles protuberant.

The name *Pseudolimnophila* was proposed for a certain group of the old genus Limnophila, including *L. luteipennis* and its allies. The adult flies closely resemble species of Limnophila, but the immature stages are very different and of a distinctly more generalized type.

The larvae are herbivores, with the mentum heavily chitinized, completely divided into two halves, the margin conspicuously toothed, the hypopharynx heavily chitinized and with numerous teeth, and the mandibles short and blunt and with many obtuse teeth. The points of resemblance to the Limnobia type are numerous, and the head capsule shows few features in common with Limnophila, in the restricted sense. The pupae have the abdomen with numerous transverse rows of setiferous tubercles bearing long setae. The genotype is *Limnophila luteipennis* O. S., of eastern North America. Other species referable to this genus are *L. inornata*, *L. contempta*, *L. nigripleura*, and *L. noveboracensis*, of the Nearctic fauna; *L. lucorum* (Meig.), of Europe; and *L. frugi* Bergr., *L. claduroneura* Speis., *L. natalensis* Alex., *L. spectabilis* Alex., and several other species, of the Ethiopian fauna.

Hart (1898 [1895]:202–204) describes the habits of *P. luteipennis* in some detail. Larvae about half grown were found on March 17, 1895, these attaining their growth and pupating on April 13. Hart ascertained by dissection that the species is a herbivore, feeding on fragments of dead vegetation, numerous diatoms of many species, and minute algae.

As in many species of the Limnophilaria and a few other groups of crane-flies, the spiracular lobes are fringed with long, delicate hairs which spread out on the surface film of the water into broad fans. The larva is unable to release itself from the hold of the water except by looping the head and the anterior end of the body around the posterior end, and drawing the latter thru this loop, repeating this action until the hairs have gone below the level of the film.

It is probable that other groups of species of the old genus Limnophila will be found to deviate from the characters of this group as now restricted. Species such as *L. hyalipennis* (Zett.), *L. nemoralis* (Meig.), and others in Europe, and *L. brevifurca*, *L. emmelina*, *L. mundoides*, *L. toxoneura*, *L. ultima*, and similar anomalous forms in America, should be investigated critically when opportunity offers.

Pseudolimnophila luteipennis (O. S.)

1859 *Limnophila luteipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 236.

Pseudolimnophila luteipennis is one of the most abundant species of the tribe, and is very widely distributed thruout eastern North America. The adult flies are common in swamps and along the marshy edges of streams and ponds. The immature stages are characteristic swamp inhabitants. They have been described in detail by Hart (1898 [1895]: 202–204). Malloch (1915–17 b:222–223) adds several supplementary notes and figures of Hart's material.

Larva.— Length, 15–18 mm.
Diameter, 1.5–1.7 mm.

Coloration light brownish yellow, slightly darker toward posterior end of body.

Body covered with a delicate appressed brownish pubescence and abundant stiff bristles and erect hairs on each segment, arranged in about five transverse rows; these bristles more numerous, coarser, and blacker, on posterior segments, forming a large tuft on sides of penultimate segment of body. Spiracular disk (Plate XXXIX, 176) surrounded by four lobes, the posterior pair very long and slender, finger-like, the lateral pair much shorter but slender; the inner face of these lobes with brownish black or dark brown transverse lines which cover almost the entire face; an arcuate line extending from ends of ventral marks across disk between spiracles; two small triangular marks located between ventral lobes; lobes fringed with long, delicate hairs, those at ends very elongate, those toward base of lobes shortened but continuous around disk. Anal gills four, very long and slender, exceeding ventral lobes of spiracular disk.

Head capsule short and stout, exhibiting a very generalized condition. Prefrons very broad, only slightly narrowed behind and but slightly exceeding lateral plates. Labrum broadly transverse, with a large tuft of hairs on either side. Mentum (Plate XXXIX, 172) completely divided, each half with seven (or rarely eight) teeth along anterior margin, of which the third (or fourth) from the inside is the largest; a flattened lobe just laterad of each half of mentum; mental plates continuous behind with strong lateral plates of capsule; in a normal position the two halves of mentum overlying each other to a greater or less degree. Hypopharynx (Plate XXXIX, 173) with anterior margin broadly rounded, with numerous (from ten to fifteen) bluntly rounded teeth. Antenna slender, with two long apical papillae. Mandible (Plate XXXIX, 175) short and broad, of the generalized limnobiine

type; tips blunt, ending in two large approximated teeth, with a row of smaller lateral teeth extending basad of each; ventral cutting edge with about four such lateral teeth, dorsal edge with one or two much larger teeth; two strong setae near base of scrobe, and two others near tip of mandible; a large brush of hairs at prosthecal region. Maxilla not projecting, with dense brushes of short, stiff hairs and with two short sensory tubercles which are tipped with very elongate setae; palpi stout and chitinized at base, the apex narrowed and pale.

Pupa.— Length, 10–13 mm.
Width, d.-s., about 1.5 mm.

Thorax reddish brown to black in color, depending on age of specimen; abdomen dirty whitish with narrow transverse brownish lines, both above and below; pronotal breathing horns dark brown or blackish.

Form subcylindrical, abdomen slightly depressed. Cephalic crest of two slender tubercles behind, tipped with long setae; another pair of setae between antennal bases. Pronotal breathing horns elongate, transversely ringed, the tips widely and deeply split into two divergent flaps. Prothorax with a prominent median carina. A tubercle in front of each breathing horn, each with about four stout setae. Mesonotum above wing axil with a tubercle bearing three setae. Wings reaching end of second abdominal segment. Legs reaching end of third abdominal segment, the tarsi ending about on a level or those of fore legs a little longer than those of other two pairs.

Abdominal segments divided into two annuli, the basal one still further subdivided into annulets; on tergum three annulets, each bearing a transverse row of setiferous tubercles, the setae very long and conspicuous, in some cases the tubercles multisetose, third annulet with two widely separated, slender, elongate tubercles. Posterior annulus with a basal and a terminal transverse row of setiferous tubercles. On sternum, four transverse rows of setiferous tubercles on basal ring and two on posterior ring. On pleura, protuberant spiracles. Lateral angles of segment 8 jutting out into stout lobes which are densely studded with setiferous tubercles, on ventral face continued toward median line as a nearly straight row of about eight setiferous tubercles, on dorsum a finger-like lobe on either side. Male cauda (Plate XL, 178) with sternal valves shorter than dorsal lobes, blunt at tips; tergal valves acutely pointed, directed dorsad. Female cauda (Plate XL, 179 and 180) with tergal valves considerably longer than the more slender sternal valves, broad medially, tapering to the broad, blunt tips which terminate in blackened points; two setae on outer margin.

Nepionotype.— Larch Meadows, Ithaca, New York, April 20, 1917.
Neanotype.— Female pupa, with type. No. 19–1917.
Paratypes.— Larvae with type. Pupae of both sexes from Bool's hillside, Ithaca, New York, June 6, 1917. A female pupa, Orono, Maine, taken as a larva June 13, 1913, emerged June 22. Female pupa, July 15, 1913, No. 75–1913.

Pseudolimnophila inornata (O. S.)

1869 *Limnophila inornata* O. S. Mon. Dipt. N. Amer., part 4, p. 219, 220.

Pseudolimnophila inornata is not so common as *P. luteipennis* but is found in similar situations. The immature stages are spent in rich organic mud. The only specimens that the writer has reared were taken in

Larch Meadows, near Ithaca, New York, on May 15, 1917, where they were associated with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, *Tipula dejecta*, and other swamp-inhabiting species.

Larva.— Very similar to that of *P. luteipennis*, but body is darker and is conspicuously blotched with whitish, especially on posterior parts of ventral segments. Mouth parts nearly the same in the two species. Antenna (Plate XXXIX, 174) with two very long and slender terminal papillae, one blunt at tip, the other much longer and tapering gradually to tip.

Pupa.— Very similar to that of *P. luteipennis*, but somewhat smaller and darker-colored. Pronotal breathing horns (Plate XL, 177) darker brown, the divergent terminal flaps proportionately a little more elongate, equal to almost one-quarter length of entire horn. Dorsal lobes at base of ovipositor more attenuated.

Nepionotype.— Larch Meadows, Ithaca, New York, May 15, 1917. No. 53-1917.
Neanotype.— Larch Meadows, Ithaca, New York, May 25, 1917. No. 53-1917, cast pupal skin.

Subtribe **Dactylolabaria**

The division Dactylolabaria is proposed for the genus Dactylolabis, a small group of curious crane-flies which are still not well understood. The adult flies bear a striking resemblance to species of the genus Limnophila, but the larvae and the pupae show characters that are not found in the more specialized divisions of the Hexatomini. The type of the genus is *Limnophila montana* O. S. of the eastern United States. Other Nearctic species included are *L. damula* O. S. (western United States), *L. rhicnoptiloides* Alex. (northwestern Canada), *L. cubitalis* O. S. (eastern United States), *L. nitidithorax* Alex. (western United States), and *L. hortensia* Alex. (western Canada).

The immature stages of two European species — *D. wodzickii* (Now.) and *D. denticulata* Bergr.— have been made known by Nowicki (1867: 340–343) and by Mik (1894), respectively. Their descriptions of the details of the larval head and the lateral spiracles of the abdomen of the pupa are incomplete, however. The larvae of none of the American species have as yet been made known, but the pupae of *D. cubitalis* O. S. were found by Needham and are described hereinafter.

Genus **Dactylolabis** Osten Sacken (Gr. *finger forceps*)

1859 *Dactylolabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

Larva.— Body very depressed, the ventral surface, especially, being greatly flattened. Head capsule compact; mentum not completely divided, its anterior margin with seven teeth. Mandible with but few lateral teeth.

Pupa.— Somewhat similar to pupae of Limnophilaria. Pronotal breathing horns short and cylindrical. In some species, at least, second abdominal segment with a very large and prominent lateral spiracle.

Dactylolabis is a small genus including about thirteen known species which are about equally well distributed in Europe and North America.

Dactylolabis denticulata (Bergr.)

1891 *Limnophila denticulata* Bergr. Mittheil. Naturf. Ges. Bern, p. 132.

The present knowledge of the life history of *Dactylolabis denticulata* is due to the work of Mik (1894), whose paper is cited by other workers, among them Grünberg (1910:54–55).

Larvae and pupae were found on the dark brownish gray chalk cliffs near Steiermark on August 3, 1891. In certain places on the cliffs were broad or narrow bands of black. The larvae and the pupae were found along these dark bands and showed a decided resemblance to their surroundings. The surface of the rock was wet with dripping water, which supported a flora of lowly plant organisms on which the larvae presumably fed. The adherence of the pupa to the last larval skin is of interest since it presumably aids in the emergence of the adult. A similar condition is found in Cylindrotoma.

Larva.— Length, 7 mm.
Width, 2 mm.

Form very depressed (Plate XLI, 183), the ventral surface flattened, almost leechlike. Both dorsal and ventral surface provided with hairs, with longer and more numerous hairs on sides of body. Body covered with small, black, structureless particles of earth or excrement, more numerous near margins of dorsal surface, these particles lacking a definite arrangement and being very firmly attached to the body hairs; when particles are removed, larva is of a greenish gray color, subhyaline. Abdominal segments divided into two rings bearing long hairs which are more conspicuous on sides of body. Head capsule (Plate XLI, 182) small but compact, completely retractile within prothoracic segment. Labrum relatively large and semitransparent, the margins with long hairs; on dorsum on either side a long delicate seta. Mentum chitinized; anterior margin with seven teeth, behind median tooth a brush of hairs. Antenna two-segmented; basal segment cylindrical; second segment button-like, with apex pointed. Mandible three-toothed; a tuft of hairs at prosthecal region. Spiracular disk surrounded by two fleshy welts which are deeply incised medially to appear as four blunt lobes. Spiracles difficult to distinguish in a position of rest, elliptical, margined with blackish brown.

Pupa.— Length, 8 mm.
Width, 1.75 mm.

Coloration blackish; abdomen dark greenish gray.

Pupa (Plate XLI, 181) attached to old larval skin, which in turn remains attached to rock surface. (Just before pupating, the larva sticks itself to the surface by means of its saliva.) Pronotal breathing horns cylindrical, a little swollen at ends. Sheaths of appendages dull and black in color. Leg sheaths attaining end of fourth abdominal segment.

Dactylolabis wodzickii (Now.)

1867 *Rhicnoptila wodzickii* Now. Verh. Zool.-Bot. Ges. Wien, vol. 17, p. 337–354.

The species *Dactylolabis wodzickii* was first found in the high Alpine region of the Hungarian Tatras, at an altitude of from 6000 to 8000 feet, in a region frequented by the wall creeper (Tichodroma). Here the adults and the immature stages were found together on the granite cliffs where water dripped continuously, supporting a considerable algal flora. Associated with the species were other flies, *Liancalus virens* (Scop.) and *Clinocera fontinalis* Hal., as well as *Tricyphona schineri* (Kol.). The degenerate wings of the insects prevent their flying, and they probably live and die close to the place where the eggs are deposited. One fly was observed laying her eggs in the masses of algae in this situation. The larvae live in these masses and pupate in them.

Larva.— Length, 12.5 mm.
Width, 2.4 mm.

Dorsum of body dark greenish brown, with dark longitudinal brown stripes producing a curious pattern of straight and convergent lines; ventral surface almost white, unmarked.

Body depressed, flattened, abdominal segments divided into a narrow basal and a much broader posterior annulus. Head capsule (Plate XLI, 185) compact, massive. Mandible showing but a single inner tooth. Posterior abdominal annuli with two long setae on lateral margins. Spiracular disk (Plate XLI, 186) surrounded by four lobes, the ventral pair longer than the others; these lobes margined with darker chitinized lines and provided with fringes of moderately long hairs. Spiracles not described, and undoubtedly overlooked by the describer.

Pupa.— Length, 12.5–13.5 mm.
Width, 2.6 mm.

Color brown. Pronotal breathing horns short, cylindrical. Wing sheaths ending opposite middle of second abdominal segment. Leg sheaths ending beyond middle of third segment. Abdomen armed with rows of spines (Plate XLI, 184).

Dactylolabis cubitalis (O. S.)

1869 *Limnophila cubitalis* O. S. Mon. Dipt. N. Amer., part 4, p. 229.

Dactylolabis cubitalis is a local species, often occurring in great numbers. In the gorge of Fall Creek near the Cornell University campus this species

can be found in myriads by sweeping the rank herbage in May. The writer has never located the immature stages, but the species was reared by Dr. J. G. Needham at Ithaca, New York, on May 20, 1898. There is no record as to where these larvae occurred, but they are presumably mud-inhabiting forms, or possibly they frequent habitats similar to those described for the two preceding species.

Pupa.— Length of cast skin, about 12 mm.

Pronotal breathing horns (Plate XLI, 187) short, cylindrical, the tips scarcely enlarged. Mesonotum behind with a prominent rounded tubercle on either side of median line, which is set with two spines, a larger outer spine and a small inner spine. Wing sheaths ending opposite apex of second abdominal segment. Leg sheaths ending opposite apex of third abdominal segment, the tarsal sheaths terminating on a common level.

Abdominal segments divided into two rings. Tergites with posterior ring having a transverse row of elongate tubercles, there being about eight on segment 2, about six on intermediate segments (3 to 5), and about four on segments 6 and 7; these tubercles fleshy, but sparsely armed with chitinized spines. Basal ring unarmed. Pleura with a strong tubercle on each ring; a blunt but prominent spiracle at extreme base of posterior ring; this spiracle very prominent on segment 2 (Plate XLI, 188), much exceeding lateral tubercles and being about two-fifths length of pronotal breathing horns. Sternites with about six tubercles on posterior ring. Male cauda (Plate XLI, 189) with tergal lobes slender, running out into acute chitinized points, which are directed caudad, slightly divergent; dorsum of segment 8 with posterior lobes powerful, about equal in size to, or a little larger than, tergal lobes of cauda just described; anterior lobes small, directed caudad and laterad; two large lateral lobes and two smaller ventral lobes. Female cauda with tergal valves moderately elongate, stout, broad at base, narrowed toward tip, where they run out into long, chitinized points directed caudad and slightly dorsad.

Neanotype.— Cast pupal skin, Ithaca, New York, May 20, 1898.
Paratype.— Pupae, cast skins, with type.

Dactylolabis montana (O. S.)

1859 *Limnophila montana* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

The species *Dactylolabis montana* is common and widely distributed thruout the northern United States. It is a characteristic inhabitant of rocky cliffs, where it rests in crevices on the almost vertical walls. The immature stages have long remained unknown, but during the spring of 1920 W. L. McAtee found a pupal skin and the teneral adult near Washington, D. C. Mr. McAtee writes that the pupa was found in the moss that covers the almost vertical north face of a cliff on Plummers Island; this moss is mostly shaded, and grows on a thin layer of black soil which, at that time of the year at least, is saturated with water. The

pupal skin was not in condition for study, but now that the larval habitat is known it is hoped that more material of the immature stages will become available.

Subtribe **Limnophilaria**

The division Limnophilaria comprises a large and heterogeneous group of species which in their larval and pupal characters grade rather insensibly into the next subtribe, the Hexatomaria, altho the adults of the two subtribes are very distinct.

The larvae of the various species in the group Limnophilae are rather similar to one another. The head capsule is long and narrow, with the lateral plates very slender. The labrum is ample, with several sensory papillae and setae. The antennae (which are two-segmented in the subgenera Phylidorea and Lasiomastix, and probably also in Dicranophragma and others) bear at their tips, in addition to the usual elongate setae, an oval or elongate-oval papilla which is delicately sculptured. The mental region is feebly chitinized, and consists of two short longitudinal bars articulated at their cephalic ends with a transverse bar which functions as the mental plate; this bar, or plate, is usually delicately grooved with parallel striae, a type of articulation that allows for great distention of the gular region in feeding. The mandibles are powerful chitinized hooks bearing two or more acute or flattened teeth at about midlength. The outer lobes of the maxillae project far cephalad as pale flattened blades.

The spiracular disk, in the primitive condition, is squarely truncated and is surrounded by five subequal lobes which are fringed with rather short hairs. The dorso-median lobe is lost in most species, but the two pairs of lobes are more or less preserved in the other species known to the writer, altho the lateral pair is sometimes reduced to a mere fringe or tuft of hairs. The terminal fringes of the ventral lobes are often greatly elongated, and fanlike. The anal gills are four in number, retractile, and rarely conspicuous. As is usual in many mud- or sand-inhabiting species of Tipulidae, the larvae are capable of greatly distending the subterminal abdominal segment. This segment is often provided with numerous transverse rows of fine points, and its inflation assists in the larva's progression thru the soil.

The larvae of the group are carnivorous, and almost without exception are exceedingly agile and snakelike in their motions.

The pupae of the group Limnophilae have the pronotal breathing horns usually small, or at least not greatly elongated. The abdomen is often greatly depressed, with the lateral margins flattened and carinate and the segments incised. In the species of the subgenus Phylidorea the segments of the abdomen are armed with rows of long, slender spines.

The group Ulomorphae seems to be closely related to the other members of the division, but the immature stages present some curious conditions which it is difficult to correlate with the same structures in the group Limnophilae. The writer has removed a group of species from the old genus Limnophila, and has placed these in the genus Pilaria Sintenis.

In the larvae of the group Ulomorphae, the epipharynx and the maxillae are densely hairy. The maxillary lobes are slender. The mandibles are hinged at about midlength, the basal segment being concave on its inner face to receive the mandibular blade when in a position of rest. The mandibular blade has one, or sometimes two, elongate acute teeth at the base. The mental region is not chitinized. The spiracular disk is surrounded by four lobes, of which the lateral pair are often very reduced; the inner faces of the lateral lobes are capable of close approximation, so that when they are closely applied the spiracles are contiguous. The pupae have the pronotal breathing horns very elongate, with their tips split into two flattened divergent lobes, as in Pseudolimnophila and a few tipuline forms.

The following keys separate the genera and the subgenera of the subtribe Limnophilaria:

Larvae

1. Mental region not chitinized; maxillae and epipharynx fringed with conspicuous, long, golden-yellow hairs; mandibles hinged; head capsule with dorsal plate spatulate at its tip. (Group *Ulomorphae*, p. 869)..2
   Mental region a narrow, transverse, chitinized bar, finely striate; maxillae and epipharynx without conspicuous hairs; mandibles not hinged; head capsule not as described above. (Group *Limnophilae*, p. 858)....................................3
2. Length under 12 mm.; basal tooth of mandibular blade nearly half the length of blade. *Ulomorpha* O. S. (p. 869)
   Length over 14 mm.; basal tooth of mandibular blade about one-third or less the length of blade..*Pilaria* Sint. (p. 872)
3. Spiracular disk almost squarely truncated, surrounded by five subequal lobes producing an eriopterine appearance.........................*Dicranophragma* O. S. (p. 861)
   Spiracular disk obliquely truncated, surrounded by two pairs of lobes of which the lateral pair are the shorter..4
4. Mandibles with two or three acute teeth at about midlength; epipharynx with a circular area bearing two biarticulate papillae........................*Phylidorea* Bigot (p. 866)
   Mandibles with three or four flattened and truncated teeth along blade; epipharynx without papillae as above..................................*Lasiomastix* O. S. (p. 863)

Pupae

1. Pronotal breathing horns very long, cylindrical, the tips split into divergent flaps. (Group *Ulomorphae*, p. 869)....2
   Pronotal breathing horns not elongate-cylindrical. (Group *Limnophilae*, p. 858)....3
2. Abdominal segments with tubercles or spines only near posterior margins of segments. *Ulomorpha* O. S. (p. 869)
   Abdominal segments with three or four pairs of blunt, naked tubercles. *Pilaria* Sint. (p. 872)
3. Abdominal segments depressed, lateral margins flattened, carinate, segments deeply incised....4
   Abdominal segments not depressed nor incised; pronotal breathing horns bicolored. *Dicranophragma* O. S. (p. 861)
4. Abdominal segments with rows of acute slender spines; pronotal breathing horns very short, semicircular in outline, bluntly rounded at their tips.. *Phylidorea* Bigot (p. 866)
   Abdominal segments without such slender spines; pronotal breathing horns short, broad, slightly compressed, tips a little pointed.... *Lasiomastix* O. S. (p. 863)

Group Limnophilae

Genus **Limnophila** Macquart (Gr. *swamp + friend*)

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1854 *Phylidorea* Bigot. Ann. Soc. Ent. France, p. 456.
1861 *Limnomya* Rond. Dipt. Ital. Prodr., vol. 4, p. 11.

Larva.— Form slender. Spiracular disk surrounded by five, or more commonly four, lobes, the ventral pair the longer and fringed with long, delicate hairs. Anal gills four, not conspicuous. Head capsule flattened, very dissected, with plates narrow. Mandible not hinged, curved, chitinized, on cutting edge with a few acute or flattened teeth. Maxilla with outer lobe produced into a flattened projecting blade. Antenna two-segmented, at its tip with a short or elongate-oval papilla which is delicately sculptured. Mentum a transverse chitinized crossbar which is finely grooved.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns usually small, flattened, tips not split. Mesonotum convex or flattened above. Abdominal segments in some cases armed with tubercles or spines.

The genus Limnophila comprises a very extensive group of crane-flies (more than one hundred and fifty species), which are found in most parts of the world but are apparently more numerous in the temperate regions. The adult flies seem to be closely related, but the immature stages are so varied in structure as to make it appear that the group must be a heterogeneous one and the similarity of the adults a result of convergent evolution.

The adult flies may be found resting on rank vegetation. Several of the species (*Limnophila ultima*, for example) swarm in small groups of from fifty to sixty individuals, copulation taking place in the air, as is discussed more fully on page 711.

The immature stages of several species have been made known, but there are still very considerable gaps in the present knowledge. The larvae are among the most carnivorous of all crane-fly larvae. The feeble chitinization of the mental region allows for great distention, and oftentimes the prey of these larvae consists of forms that are nearly as large as the captors themselves.

The data regarding extra-American species may be summarized as follows:

Limnophila bryobia Mik (1881:205–206) was reared from moss, taken in the Auckland Islands, near New Zealand, in the summer (December to February) of 1874–75. The moss was dried and then placed in a temperature of from 12° to 15° Réaumur. In March of 1879 an adult fly appeared. This long interval of more than four years was supposed by Mik to have been passed by the insect as a larva, the dry moss furnishing the food. Possibly the eggs were carried over for a long period before hatching.

Limnophila sinistra Hutton, of New Zealand, has been discussed in some detail by Hudson (1920:33–34), who states that this species is common in most dense forests thruout the country. The larva inhabits fallen tree-trunks in an advanced state of decay, forming burrows between the soft, decayed part and the harder part of the wood. It is about 25 millimeters in length, cylindrical, tapering toward the head, which is very small, and furnished with two minute jaws and a pair of very short antennae. There are eleven visible body segments. The extremity of the last segment is truncate and deeply excavated, the concavity being protected by five converging spines, which can be spread out or drawn inward at the will of the insect. Pedal warts occur on the undersides of all the segments except the three immediately following the head and the terminal segment. The pupa is about 12 millimeters in length, and rather stout. The breathing horns are about one-third the length of the wing sheaths, and are moderately stout and strongly recurved. There are two dorsal rows of hooks on each exposed abdominal segment and one ventral row near the terminal extremity. The valves of the ovipositor are strongly recurved and very stout. The head and the thorax are dark brownish black, highly polished; the abdomen is grayish ocherous, darker in the middle; the ovipositor and the terminal segments of the posterior tarsi are reddish. The pupa rests in a burrow made by the larva near the surface of the log.

Edwards has decided that this insect and a few related species should be placed in a new genus. The affinities of the fly, to judge from the details supplied by Hudson, are with the Epiphragmaria rather than with the Limnophilaria, but until more details are forthcoming it cannot be definitely referred to that division.

Limnophila (*Phylidorea*) *ferruginea* (Meig.), of Europe, is closely allied to *L. adusta* (page 867), and is of especial interest as being the type of the subgenus Phylidorea. It was reared by De Meijere (1916:204–206) from larvae found living between saturated decaying leaves along the banks of watercourses. Further mention of the species is made under the discussion of the subgenus Phylidorea (page 866).

Limnophila hyalipennis (Zett.), of Europe, was found by Beling (1886: 198–199) in piny woods, where the larvae live in old ant hills or in piles of earth thrown up by wagon wheels. The apparent lack of pupal breathing horns in this species is discussed on page 755. The European species *L. lineola* (Meig.) (Beling, 1879:54 and 1886:199–200), *L. nemoralis* (Meig.) (Beling, 1886:200–201), and *L. ochracea* (Meig.) (Beling, 1886: 202) are all found in damp earth along the margins of woodland streams or in damp spots in the woods. Larvae of *L. dispar* (Meig.) were found by Perris (1849:331) living in the hard, withered stalks of an umbellifer, *Angelica sylvestris* Linn., where they hollowed out long passages in the pith. (This reference is cited by Mik, 1881:204, and by Osten Sacken, 1869:201–202.) *Limnophila pallida* Bel. was reared by Beling (1873a: 557) from larvae living in a decaying ash trunk.

The reference to *Limnophila platyptera* Macq. given by Heeger (1854) is considered by Osten Sacken (1869:4, 202) to refer to a mycetophilid, probably Bolitophila.

The American species that are now known are considered in the following pages. In addition, *Limnophila unica* O. S. has been bred from larvae found in decaying wood.

It is very probable that some of the species listed above, as well as many of the limnophiline forms that are still unknown as regards their immature stages, will be found to belong to some one or other of the remaining divisions of the tribe, rather than to the Limnophilaria as here restricted. This group requires more careful study than does any other division of crane-flies.

(Subgenus **Dicranophragma** Osten Sacken)

1859 *Dicranophragma* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

Larva.— Form short and stout. Spiracular disk surrounded by five short lobes, the ventral pair the longest, the dorsal lobe very blunt; disk surrounded by a fringe of delicate hairs which are longest at tips of lobes. Head capsule of the hexatomine type. Mandible powerful, prolonged into a strong hook with a large acute tooth just beyond midlength. Maxilla very long and slender. Mentum chitinized, consisting of a narrow transverse bar which is ribbed with fine parallel grooves.

Pupa.— Cephalic crest prominent, each half with three setae. Pronotal breathing horns short, cylindrical, or slightly narrowed to a blunt tip. Mesonotum convex, unarmed. Wing sheaths short, broad, ending before tip of second abdominal segment. Leg sheaths moderate in length, ending just beyond base of fourth abdominal segment, hind tarsi a little longer than the others. Abdominal segments divided into two rings; posterior ring with a subterminal transverse armature, on dorsum consisting of numerous setiferous tubercles, on pleura consisting of two or three groups of setiferous tubercles; basal ring with about eight slender tubercles on dorsal surface. Spiracles present, but evidently nonfunctional. Dorsum of segment 8 with four slender tubercles.

Dicranophragma is a well-defined group of the genus Limnophila, with about six known species whose center of distribution seems to be in the Oriental region. The type of the subgenus, *Limnophila* (*Dicranophragma*) *fuscovaria*, discussed in detail below, is the only described New World form. The immature stages are spent in rich organic mud in cool, shaded woods.

Limnophila (*Dicranophragma*) *fuscovaria* O. S.

1859 *Limnophila* (*Dicranophragma*) *fuscovaria* O. S. Proc. Acad. Nat. Sci. Phila., p. 240.

The adult flies of *Limnophila fuscovaria* may be easily distinguished by their broad, heavily spotted wings and the strong supernumerary crossvein in cell R_2. They may be swept from rank vegetation in cool, shaded woods. The larva has the body stouter and less elongate than is usual in this group of species, but it possesses the same snakelike movements as its near relatives. The pupal duration is not longer than eight days (June 8 to 16, in 1917).

Larva.— Length, 6.8–7.2 mm.
Diameter, 0.7–0.8 mm

Coloration light golden-yellow; maxillary lobes yellow; spiracular disk lined with dark brown. Body rather short and stout, not of the exceedingly elongate type of the Eriopterini, gradually narrowed to anterior end (Plate XLII, 190); prothoracic segment truncated anteriorly;

when head is retracted, tips of maxillae projecting from prothoracic orifice. Seventh abdominal segment with a transverse fringe of stiff hairs on the sides, these directed laterad and slightly caudad. Body noticeably constricted just before last segment. Spiracular disk (Plate XLII, 195) surrounded by five lobes, and in superficial appearance decidedly eriopterine rather than hexatomine; ventral lobes the longest but still much shorter than is usual in this tribe, slightly divergent, inner face with a double, V-shaped, dark brown mark, inner arm of V narrow, outer arm more expanded, especially at proximal ends, one large inner and two smaller outer sensory bristles at apex of V; lateral lobes narrow, with a V-shaped mark similar to that of ventral lobes but narrower and darker; dorsal lobe broad, the inner face indistinctly lined with parallel, dusky, longitudinal stripes; all five lobes surrounded by a fringe of long, delicate hairs lying just outside brown marks, these hairs longest at tips of lobes and continuous around disk. Spiracles circular, rather widely separated; ring broad, light yellow, narrowly margined outwardly with black. Anal gills four, short and stout.

Head capsule (Plate XLII, 191) very dissected, consisting of six elongate slender plates, three on either side, articulating at a point laterad of mental plate. Labrum (Plate XLII, 192) large; anterior margin indistinctly trilobed, the median lobe hairy; on the ventral, or epipharyngeal, surface, on either side, a slender cylindrical papilla, subhyaline, directed cephalad; sides of epipharynx with a tuft of long setae. Mentum chitinized, consisting of two lateral rods and an anterior transverse bar which is finely ribbed with parallel lines. Immediately dorsad of mentum two roughened papillae (prementum) directed cephalad; esophagus retrorsely roughened. Antenna (Plate XLII, 193) stout, in caustic-potash preparations almost hyaline, tipped with an elongate cylindrical lobe distad of which is a small setiferous tubercle with two long, delicate setae exceeding antennae in length. Mandible (Plate XLII, 194) powerful, very deep at base, produced into an acute, strongly curved tip; just beyond midlength a very large, acute tooth which is about one-third length of apical point, in its angle a small, hyaline, flattened, leaflike blade with a truncated apex; basad of large tooth two or three gradually smaller teeth. Maxilla with outer lobes stout, broad at base, gradually narrowed to tip, which is cut off by a constriction into a semi-oval structure; palpi on inner dorsal face of maxillary lobe at about midlength, short, semi-globular, with abundant sensory papillae; when head is completely retracted, the long, pale, slightly divergent tips of maxillary lobes projecting from orifice.

Pupa.— Length of cast skin, about 6 mm.

General coloration dark brown; pronotal breathing horns almost black, with apical fourth conspicuously light yellow; abdominal incisures pale.

Cephalic crest large and prominent, with three long setae on outer face. Labrum blunt at apex. Labial lobes with a blunt point on either side, these directed proximad and caudad. Maxillary palpi broad at base, suddenly narrowed to the long, cylindrical tip, which is darkened. Antennae rather short. Pronotal breathing horns (Plate XLIII, 196) stout, short, almost straight, broad basally, tapering gradually to the blunt tips. Wing sheaths very short and broad, ending before tip of second abdominal segment. Leg sheaths short, extending to just beyond base of fourth abdominal segment; all the tarsi ending about on a level, or outer sheaths a little the longer.

Abdominal segments (Plate XLIII, 198) each divided into two rings by a false constriction, basal ring about two-thirds length of posterior ring. Basal ring on dorsum with a transverse row of about eight slender, blunt tubercles before caudal margin; on pleura a similar but larger tubercle opposite basal ring, this tipped with a long, delicate seta. Sternum unarmed. Posterior ring on dorsum with a subterminal row of blunt tubercles, simple or bifid, often approximated or crowded, bearing one or two long setae; near base of tergum, opposite spiracle, a setiferous tubercle; on pleura, opposite base of posterior ring and nearer dorsum than sternum, a vestigial spiracle with a double setiferous tubercle ventrad of it; near caudal margin of pleura two or three compound multisetose tubercles (Plate XLIII, 197) or aggregations of simple tubercles, which are largest on seventh segment. On sternum, two slender tubercles on either side, near base of posterior ring. Female cauda (Plate XLIII, 201) elongate, with the tergal valves a little longer than the sternal valves; each of tergal valves with a small tubercle at base. Male cauda (Plate XLIII, 199 and 200) with the ventral lobes blunt, the dorsal lobes a little longer and ending in an acute point; a tiny tubercle on either side at base of dorsal lobes. Dorsum of segment 8 with a trapezoid of four conspicuous lobes ending in truncated tubercles; anterior pair of lobes smaller and a little more widely separated than posterior pair.

Nepionotype.— Ithaca, New York.
Neanotype.— Ithaca, New York, May 31, 1917. No. 57–1917.
Paratypes.— Pupal skins, June 11, 1917 (No. 99-1917), June 16, 1917 (No. 132-1917). Abundant larvae, with nepionotype.

(Subgenus **Lasiomastix** Osten Sacken)

1859 *Lasiomastix* O. S. Proc. Acad. Nat. Sci. Phila., p. 233.

Larva.— Body slender, with pencils of stiff setae on lateral margins of thorax. Spiracular disk with four lobes, the ventral pair a little the longer and bearing a fringe of long, delicate hairs, these about twice length of lobes. Anal gills short and stout. Head capsule of hexatomine type. Mandible powerful, cutting edge with a single row of three or four flattened, bladelike teeth. Maxilla very long and slender. Antenna elongate, at tip with a small elongate-oval papilla whose surface is delicately sculptured. Mentum chitinized, a strong transverse bar which is ribbed with fine parallel grooves.

Pupa.— Cephalic crest very small, inconspicuous, bilobed. Pronotal breathing horns short, broad, somewhat compressed, a little pointed at apex. Mesonotum unarmed. Abdominal segments depressed, armed with numerous tubercles or small spines, these being most abundant on posterior annuli of segments.

The subgenus Lasiomastix includes but six known species, three of which are from eastern North America. *Limnophila* (*Lasiomastix*) *macrocera* is common and widely distributed thruout the Eastern States. *L.* (*L.*) *tenuicornis* O. S. and *L.* (*L.*) *subtenuicornis* (Alex.) are found only in the Northeastern States and are more local in their distribution. The immature stages of *L.* (*L.*) *macrocera* are spent in rich organic mud. They are very similar to those of the subgenus Phylidorea.

Limnophila (Lasiomastix) macrocera (Say)

1823 *Limnobia macrocera* Say. Journ. Acad. Nat. Sci Phila., vol. 3, p. 20.

Limnophila macrocera is a common swamp-inhabiting crane-fly, the larvae living in organic mud. At Orono, Maine, the writer found larvae of this species associated with larvae of *Bittacomorpha clavipes*, *Pilaria tenuipes*, *P. recondita*, *Erioptera chlorophylla*, and other crane-flies, as well as with leeches, snails, worms of many kinds, and other forms of life. The larva is similar to that of other related species. When placed in water it is very active and has the habit of darting the anterior quarter of its body from one side to the other, suggesting the striking of a reptile. The pupal duration is not more than eight days (June 24 to July 2, June 28 to July 6).

Larva.— Length, 14.5–15 mm.
Diameter, 1.4 mm.

Coloration, pale yellowish white.

Body terete, narrowed toward both ends but more noticeably toward anterior end. Integument covered with a dense appressed pubescence. Chaetotaxy as follows: two stout setae on both dorsal and ventral margins of prothoracic orifice; thorax with pencils of stiff setae near anterior margins of segments, two large lateral tufts and a smaller ventral pair; abdominal segments with a pencil of similar bristles on ventro-lateral margins, one on anterior half, the other midlength, of each ring; a seta at posterior lateral angles of sternites; four setae in a transverse row near posterior margin of tergites, the lateral pair the larger; lateral margins of cauda near base of lateral lobes and above gills with pencils of blackish setae; basal part of segments on both sternum and tergum with transverse parallel rows of fine scabrous points, this area very narrow on second abdominal segment, consisting only of three or four rows, the areas gradually becoming broader and the rows more numerous, there being on sixth and seventh segments about 28 to 30 rows which occupy nearly the basal third of segments.

Spiracular disk (Plate XLIV, 208) surrounded by four lobes; ventral pair the longest, lateral pair a little shorter; ventral lobes near tips with a brush of delicate, exceedingly long hairs which curl into loops at tips, the longest of these hairs about twice length of lobes bearing them; this fringe of hairs continuous around disk, longest at ends of lobes, gradually shortened toward their bases but not interrupted; lateral lobes with terminal hairs a little shorter but still longer than lobes themselves; inner faces of lobes delicately margined with dark brown, those of ventral lobes having the outer lateral margins the broadest. Spiracles rather small, located at base of lateral lobes. Anal gills four, very stout and plump.

Head capsule with a framework of long, slender plates, as is usual in this group. Labrum (Plate XLIV, 205) broadly transverse; anterior margin irregularly rounded; anterior median area truncated, with the lateral angles slightly projecting, cut off squarely, each with a small, hyaline, sensory papilla; laterad and caudad of each, two sensory papillae, the innermost elongate-cylindrical, more than twice length of short, oval, outer one. Epipharyngeal

region roughened by tiny groups of parallel ridges. Mental region consisting of a heavily chitinized transverse bar which is delicately grooved, enlarged at ends, and articulating with a small ventral bar. Antenna (Plate XLIV, 206) long and slender; basal segment short and broad; second segment elongate-cylindrical, bearing at its tip a small, hyaline, sensory papilla which appears delicately crosshatched by fine impressed lines, this papilla elongate-oval with the apex broadly rounded; a long hair near base of this papilla and about twice its length. Mandible (Plate XLIV, 207) long and powerful, the tip produced into a slender point, the cutting edge at about midlength with a single row of three or four flattened, bladelike teeth which are truncated at their tips, these teeth varying considerably in their shape and relative proportions. Maxilla with outer lobe elongate, the base strongly chitinized, this chitinized part continuing up margin of lobe almost to tip, the apical part nearly hyaline; at about midlength, the small palpus and a long seta. Esophagus enlarged, the walls thickened and roughened.

(A slide of a larva that was supposed to belong to this species differs considerably from the material described above. The antenna is much shorter, with the apical tubercle much larger and elongate-cylindrical; the mandible has the teeth fewer and more acute, quite as shown by De Meijere for *Limnophila* [*Phylidorea*] *ferruginea*. It is probable that this species likewise is a Phylidorea.)

Pupa.— Length, 14–16 mm.
Width, d.-s., 1.8–2 mm.
Depth, d.-v., 1.9–2.2 mm.

Breathing horns pale whitish brown, a little darker at base; remainder of body dark brownish black, abdomen a little lighter-colored; incisures of segments, and pleural line, pale.

Cephalic crest very small, inconspicuous, bilobed, each principal lobe subdivided into two smaller lobes terminating in a small seta; another seta on anterior face. Labrum rather blunt and truncated at apex. Labial lobes terminating in sharp points projecting proximad. Maxillary palpi short and stout, tapering to blunt tips (Plate XLV, 210). Antenna of male elongate, reaching to beyond midlength of wing sheath; antenna of female short, ending at about one-fourth length of wing sheath. Segments of antenna cylindrical, unarmed.

Pronotal breathing horns (Plate XLV, 209) short, broad, somewhat compressed, a little pointed at tip. Thorax broad and deep, the pronotum flattened, carinate medially. Mesonotum high, convex, transversely wrinkled. Wing sheaths ending some distance before tip of second abdominal segment. Leg sheaths short, ending before tip of third abdominal segment, the hind legs a little longer than the other legs, which end about on a common level.

Abdomen depressed, lateral margin carinate. Abdominal segments distinct, incised, each segment divided into two annuli, basal one about half length of posterior one. Basal ring on dorsum with a transverse single, or somewhat double, row of small subacute spines, which are more numerous and larger on mid-dorsal area. Pleura unarmed. Sternum with an oblique flattened lobe or wing on each side, directed caudad and proximad; between these lobes a more or less broken transverse row of from six to twelve slender tubercles. Posterior ring on dorsum with numerous small scattered tubercles. Pleura with a small circular spiracle near base and close to dorsal margin; a slender seta near spiracle and ventrad of it;

two other setae caudad of spiracle; at caudal margin a solitary seta close to ventral margin. Sternum with scattered slender tubercles, on segment 3 these appearing as a longitudinal row of about ten alongside the hind legs; between this lateral longitudinal row and the scattered discal tubercles, a bare space, at anterior end of which is a large, stout, setiferous tubercle; a subterminal transverse row of about fifteen acute black spines; on terminal segments the lateral longitudinal rows interrupted, or, on the seventh segment, lacking, on seventh segment the subterminal armature of both dorsum and sternum more powerful, especially the intermediate spines of sternum, which are very large; numerous setae scattered along rows. Segments 3 to 8 on ventral surface of posterior ring with a circular disklike area, median in position and at about two-thirds length of ring. (In some specimens, especially females, the discal tubercles on the posterior ring are much smaller and lie in longitudinal rows.) Male cauda (Plate XLV, 211) with tergal valves slender, elongate, slightly divergent, tapering to the acute tips, which bear a small subterminal seta; sternal valves short, blunt, with a flattened oval lobe between valves of sternum; eighth segment on dorsum with a trapezoid of four very long, slender, pointed lobes, which are provided with delicate hairs, the posterior pair of lobes longer, stouter, and lying closer together; just above anterior pair of lobes a blunt setiferous tubercle; pleural region of segment 8 with two spines; a small seta cephalad of these spines; sternal region of segment 8 with two widely separated setiferous tubercles. Female cauda (Plate XLV, 212) with tergal valves elongate, narrowed at tips, and armed with sharp, black spines; a few small setae before tips; sternal valves short, blunt, narrowed at tips.

Nepionotype.— Orono, Maine, July 19, 1913.
Neanotype.— With type larva, July 17, 1913.
Paratypes.— Larvae, with type larva, June 13 to July 27, 1913. Pupae, June 9 to July 22, 1913.

(Subgenus **Phylidorea** Bigot)

1854 *Phylidorea* Bigot. Ann. Soc. Ent. France, p. 456.

The immature stages of the type species of Phylidorea, *Limnophila* (*Phylidorea*) *ferruginea* (Meig.), were described by De Meijere (1916: 204–206). In Holland, larvae were found in April on the banks of a ditch, where they were living between decaying leaves. The larvae are cylindrical, and are from brownish yellow to brown in color. The antennae are described as three-segmented, the apical papilla being considered as a segment. The labrum bears on the epipharyngeal surface a median projection provided with two conspicuous biarticulate lobes. The outer lobes of the maxillae project as flattened blades. The mandibles are powerful and strongly curved, and have a group of small lateral teeth at about midlength.

The pupa is about 10 millimeters long and is blackish brown in color. The pronotal breathing horns are almost semicircular and are yellowish

brown in color. The abdomen is depressed, with sharp lateral margins. The abdominal armature is described as consisting of small hairs instead of slender spines as in the American species of this subgenus.

In the Nearctic fauna, the subgenus Phylidorea includes *Limnophila adusta*, *L. similis* Alex., *L. novae-angliae* Alex., *L. lutea* Doane, *L. terrae-novae* Alex., *L. costata* Coq., *L. fulvocostalis* Coq., *L. insularis* Johns., and probably other western species. It seems quite possible, moreover, that the species allied to *Limnophila lenta* O. S. also belong here.

Limnophila (*Phylidorea*) *adusta* O. S. (supposition)

1859 *Limnophila adusta* O. S. Proc. Acad. Nat. Sci. Phila., p. 235.

A larva of a crane-fly that is almost certainly a member of this genus was taken at Ithaca, New York, on May 30, 1917, in company with a Ulomorpha (No. 88–1917). An unknown pupa was taken in the sedge association on the Bool hillside, Ithaca, on June 4, 1917. It was not reared and its identity can only be surmised, but there can be little doubt of its relationship with Phylidorea.

Larva.— Length, 8.6–9 mm.
Diameter, 0.8 mm.

Coloration a deep saturated orange-yellow, the body with silky iridescent reflections.

Body a little narrowed at both ends. Integument with a long, appressed, golden pubescence. Numerous long setae and pencils of hairs on body, usually at about midlength of, or on posterior half of, the segments; posterior margin of each segment elevated into a prominent transverse ridge of hairs. Spiracular disk surrounded by four lobes, ventral pair about twice length of lateral pair; ventral lobes with a rather narrow, dark brown line on inner face; outer margin fringed with very long dark hairs which are somewhat paler at their bases, this fringe of hairs longest at tips of lobes, where it reaches a length of about eight or ten times length of lobe; hairs shorter toward base of lobe; a stiff sensory bristle on outer face of lobe, rather far back from tip; lateral lobes similar, with the fringe of hairs yellow and about twice length of lobes. Spiracles of medium size, directed toward each other. Anal gills four, fleshy, pale in color, posterior pair longer than anterior pair.

Head capsule of hexatomine type, the dorsal plates narrowly interrupted on mid-dorsal line behind clypeal-labral sclerite. Labrum very large, anterior margin provided with eight or ten papillae and setae. Epipharyngeal region having a large, median, circular area which is slightly elevated and bears two bisegmented cylindrical papillae. Mental region as usual in the genus, consisting of three hinged bars forming three sides of a rectangle, the anterior transverse bar delicately grooved. Antenna two-segmented, second segment narrower than first and bearing at its tip an elongate sculptured papilla and a long seta. Mandible of hexatomine type, a powerful curved hook, at about midlength of which is an

acute tooth; in axil of latter a small flattened blade which is slightly widened outwardly and has the tip truncated. Maxillary lobe broad at base, tapering to narrow tip.

Pupa.— Length, 12 mm.
Depth, d.-v., 1.6 mm.

Similar to *Limnophila macrocera* in general shape and color, differing as follows:

Labrum broadly obtuse at tip. Pronotal breathing horns (Plate XLIII, 203) very short, stout but flattened, constricted beyond midlength, and with a row of breathing pores around apex; pronotum and mesonotum carinate medially in front; wing pad showing venation rather clearly, cell M_1 deep, basal deflection of Cu_1 beyond midlength of cell *1st* M_2. Abdominal segments with lateral margins very deeply incised, the carinate lateral margins very accentuated, appearing as thin, flattened wings (Plate XLIII, 204). Armature of abdomen consisting of abundant elongate, acicular spines, some of which are sinuously twisted; on basal ring these spines appearing as a subterminal transverse row on both dorsum and sternum; on posterior ring, besides the subterminal transverse row, spines are scattered over surface in more or less distinct longitudinal rows; at lateral carina a group of about a dozen long spines at caudal margin, as well as a powerful spine below level of spiracle on extreme margin of carina; ventrad and caudad of this, three long setae, two close beneath spine and the third underneath spiracle. Female cauda (Plate XLIII, 202) about as in *Limnophila macrocera*, but sternal valves divergent at their tips; eighth segment with a trapezoid of dorsal lobes about as in *L. macrocera*, but sternum with four stout spines bearing setae on their sides; a blunt median lobe near base of eighth sternite.

(Described from a female pupa taken on Bool's hillside, Ithaca, New York, on June 4, 1917, where it was associated with a characteristic swamp-inhabiting crane-fly fauna — *Bittacomorpha clavipes*, *Pseudolimnophila luteipennis*, *Limnophila macrocera*, *Pilaria recondita*, and *Prionocera fuscipennis*.)

(Subgenus **Limnophila** Macquart)

1834 *Limnophila* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 95.
1863 *Poecilostola* Schin. Dipt. Austriaca, vol. 2, p. 551.

Limnophila is the typical subgenus of the group, the type having been designated as *Limnophila pictipennis* by Westwood in 1840. No species of this subgenus have yet been described from North America.

The larva of *L. punctata* (Meig.) was described by Beling (1886:195–197) and by Gerbig (1913:158–161) as living in wet earth, by Scheffer (1848:10) and by Cameron (1917:63) as living in decaying wood. Gerbig found larvae in sandy soil near both standing and flowing water. The larvae are very active, are rust-brown in color, and attain a length of 15 millimeters with a diameter of from 1.5 to 2 millimeters. The body is provided with several setae and setiferous projections. The spiracular disk (Plate XLVI, 214) is surrounded by four subequal lobes and an additional reduced dorso-median lobe; all of these lobes are fringed with long

hairs, and each of the four paired lobes has a sensory bristle near the tip. The four anal gills are not very prominent.

The head capsule is of the hexatomine type. The mandibles are sickle-shaped, with two small, broad, blunt, sawlike teeth just beyond midlength.

Brauer (1883:55) found the larvae of another species — *L. pictipennis* (Meig.), the type of the genus — between wet decaying leaves in bogs. His figure of the head capsule (1883, pl. 1, fig. 10) shows a typical hexatomine head (Plate XLVI, 213). Beling (1879:51–52) found this species in the sand of a small, dried-out brook bed.

Group **Ulomorphae**

Genus **Ulomorpha** Osten Sacken (Gr. *Ula* + *shape*)

1869 *Ulomorpha* O. S. Mon. Dipt. N. Amer., part 4, p. 232.

Larva.— Form slender. Body covered with a rich golden-yellow pubescence. Spiracular disk surrounded by four unequal lobes, the ventral pair the longest, lying subparallel, fringed with exceedingly elongate hairs. Spiracles small. Head capsule narrow, the dorsal plate narrow, at tip expanded into a spatula. Mandible hinged, blade very long and slender, with a single very long lateral tooth at its base. Maxilla densely golden hairy, outer lobe projecting, bladelike. Antenna with a very long, tapering, apical papilla. Mentum not chitinized.

Pupa.— Cephalic crest prominent, each lobe with three setae. Pronotal breathing horns very long and slender, sinuous, cylindrical, at apex split into two flattened divergent lobes. Mesonotum short, very convex, unarmed. Wing sheaths attaining end of second abdominal segment. Leg sheaths short, ending before tip of third abdominal segment; hind tarsi a little longer than the others. Abdominal segments divided into two rings, posterior ring with a subterminal transverse armature of stout black spines and a few long setae; sternal armature stronger than that of dorsum. Pleura armed with a few similar spines. Acidothecae of ovipositor very long and slender. Dorsum of segment 8 with a trapezoid of four lobes.

The genus Ulomorpha includes five known species, the genotype, *Ulomorpha pilosella*, of the eastern United States, and four western North American species. The immature stages of the genotype are spent in rich organic mud in shaded situations.

Ulomorpha pilosella (O. S.)

1859 *Limnophila pilosella* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.

Ulomorpha pilosella is not uncommon in cool Canadian woods thruout northeastern North America, and the adult flies may be swept from

rank vegetation in such haunts. The flies bear a marked resemblance to the species of the subgenus Lasiomastix of the genus Limnophila, but the pupae, especially in the structure of the pronotal breathing horns, are quite distinct. The larvae are different from the related and somewhat similar larvae of the subgenus Dicranophragma of the genus Limnophila, of Penthoptera, and of similar hexatomine genera, in their pale whitish yellow coloration instead of the deep saturated yellows and oranges of the genera mentioned. All, however, have the quick, restless movements so characteristic of this group of crane-flies. Larvae found on Bool's hillside, Ithaca, New York, on May 14 and 23, 1917, transformed to adults on June 9.

Larva.— Length, 8.5–9 mm.
Diameter, 0.5–0.6 mm.

Coloration pale whitish yellow, the eighth abdominal segment suddenly whitish.

Form slender. Body covered with a dense golden-yellow pubescence. A transverse fringe of stiff, erect, short hairs at posterior margin of prothorax. A number of pencils of setae or solitary bristles on sides of segments, one on each annulus, longest near posterior margins of segments. Behind these setae, tufts of small hairs. Spiracular disk (Plate XLVI, 219) surrounded by four lobes; ventral pair the longest, lying subparallel to each other, outer margin fringed with long, delicate hairs, those near tip coarse and easily broken, some of the hairs at tips exceedingly elongate; inner face of ventral lobes heavily suffused with dark brown, this color more intense proximally; lateral lobes short, with an apical fringe of coarse yellowish setae. Spiracles very small, widely separated, located at base of lateral lobes. Anal gills four, very slender, pale in color, the posterior pair a little the longer. On sternum of eighth abdominal segment, before gills, a transverse row of four long, coarse setae.

Head capsule (Plate XLVI, 215) very long and narrow, the dorsal plate slender, at end expanded into a spatula; lateral plates a little shorter than dorsal plate. Labrum (Plate XLVI, 216) and epipharynx broadly transverse, projecting, the anterior margin narrower, truncated, on either side near base with a brush of long hairs; disk of epipharyngeal region with four setae, posterior pair a little the closer together; a few tiny papillae on ventral surface; clypeal region emarginate, with two large setae near anterior margin and another immediately behind base of antenna. Mental region not readily distinguishable in the material available, but at the most with little or no chitinization. Antenna (Plate XLVI, 217) with basal segment cylindrical, a little narrowed medially, the truncated apex with about two or three long setae and a very long, hyaline, sensory papilla which tapers gradually to apex, this papilla about three times length of segment bearing it. Mandible (Plate XLVI, 218) hinged, the base slender but powerful, with the inner face deeply concave to receive mandible in a position of rest; blade of mandible produced into a very slender hook which is almost straight, a little curved at extreme tip, at its base a very large, acute, flattened blade which is more than half length of mandible itself; in its angle this blade has a second, microscopic, tooth; prostheca with about five long, stout, comblike teeth exceeding the mandible in length, and an additional shorter, flattened blade marked with parallel grooved

lines. Maxilla with dense tufts of long yellow hairs; outer lobe produced cephalad as a hyaline, flattened blade which projects from prothoracic orifice when head is retracted.

Pupa.— Length, 8.5–9 mm.
Length of pronotal breathing horns, nearly 2 mm.
Width, d.-s., 1 mm.
Depth, d.-v., 1 mm.

Head, thorax, and appendages dark brown; pronotal breathing horns similar, but terminal half gradually paler, the tip almost yellow; abdomen pale brown.

Cephalic crest consisting of two prominent lobes, each with three strong setae, the most ventral directed outward; just before primary crest and lying between antennal bases, a very low, slightly bilobed crest which is not setiferous. Labrum elongate, obtusely rounded at apex and separating labial lobes, the latter produced caudally into subacute points. Maxillary palpi stout at base, narrowed to tip (Plate XLVII, 221). Antenna short (in female sex, at least), extending but a short distance beyond knee joints of fore legs. Pronotum (Plate XLVII, 220) high, feebly carinate medially. Breathing horns separated basally, very long and slender, sinuous, transversely wrinkled, at tip split into two flattened divergent lobes (Plate XLVII, 222 and 223). Mesonotum very short and convex, with numerous black dots which are most abundant anteriorly. Two small setae on either side behind wing axilla. Lateral angles of mesonotum blunt, but tip produced into a slender setiferous tubercle. Wing sheaths ending opposite tip of second abdominal segment. Leg sheaths short, ending just before tip of third abdominal segment, hind legs a little longer than others.

Abdomen with a narrow basal ring and a much broader posterior ring, the latter armed before posterior margin with a transverse row of small black spines, strongest on pleura, weakest on dorsum; on dorsum (Plate XLVII, 224) the spines reduced in number, there being from one to five (or in some cases none), and occurring only at or near ends of row; ends of row with two setae; on either side of median line a group of three closely approximated setae; usually segments 2 and 3 have the spines weak or lacking; segments 4 to 6 with two spines, and segment 7 with one spine, but in some specimens the number is slightly increased. Sternites (Plate XLVII, 225) with the intermediate segments (4 to 6) having about twenty spines in an almost continuous row which as a rule is uninterrupted; at each end of row about two strong setae; near base of posterior ring a narrow transverse area with two setae at each end. Pleura with a few powerful spines, small or lacking on basal segments, larger and more numerous on posterior segments, there being usually two on segment 4, three on segments 5 and 6, and four on segment 7; on pleura at about mid-length of posterior ring and nearer dorsal side, three black setae in transverse alinement, these somewhat longer on basal segments; opposite basal ring a stout seta. Female cauda (Plate XLVII, 226) elongate; tergal valves slender, slightly upcurved, near apex with a sharp black spine which is directed dorsad, laterad, and caudad; two weak setae on either side before apex. Dorsum of segment 8 with four lobes; posterior pair elongate, slender, curved, and divergent; anterior pair blunt, small, and more approximated; just ventrad of these lobes a stout seta; pleural region with two powerful spines, above the more dorsal of which is a stout seta; a seta near ventral margin.

Nepionotype.— Ithaca, New York, May 30, 1917. No. 88–1917.
Neanotype.— With type larva, reared June 9, 1917.
Paratypes.— Larvae, May 30, 1917. Pupa, June 13, 1917.

Genus **Pilaria** Sintenis (Lat., derived from *the long antennal verticils*)

1888 *Pilaria* Sintenis. Sitzber. Nat.-Ges. Dorpat., vol. 8, p. 398.
1919 *Eulimnophila* Alex. Cornell Univ. Agr. Exp. Sta., Mem. 25, p. 917.

Larva.— Form moderately slender. Spiracular disk surrounded by four unequal lobes, lateral pair in some cases very reduced, elongate ventral lobes fringed with long hairs. Head capsule of Ulomorpha type. Mandible hinged, blade with one or two acute teeth at base. Maxilla densely hairy. Mentum not chitinized.

Pupa.— Pronotal breathing horns elongate-cylindrical, tips split into flattened lobes. Abdominal segments with three or four pairs of naked tubercles.

The genus Pilaria includes a group of species of the old genus Limnophila, comprising *Limnophila tenuipes* and *L. pilicornis* and their allies. Its relationships are plainly with Ulomorpha rather than with Limnophila. The genotype is *Limnophila pilicornis* (Zett.), of northern Europe. Other included species are *L. tenuipes*, *L. recondita*, *L. imbecilla* O. S., *L. edwardi* Alex., *L. quadrata*, *L. stanwoodae* Alex., and *L. osborni* Alex., of North America, and *L. discicollis* (Meig.), *L. fuscipennis* (Meig.), *L. subtincta* (Zett.), and probably other species, of Europe.

The immature stages are spent in mud or moist earth. In Europe, *Pilaria discicollis* (Plate XLVIII, 232) has been found by Gerbig (1913: 163–164) and by Cameron (1917:63). *P. fuscipennis* is described by Beling (1886:197–198) as living in mud near a ditch. Gerbig (1913:164–166) found the larvae (Plate XLVIII, 231) in a similar situation. Brauer (1883:54) describes them as living between decaying leaves in swamps. Cameron (1917:63) states that the larvae are found in decaying wood, this record possibly being an error. According to Beling, the pupal duration is not more than ten days. In America, *P. tenuipes* has been discussed by Hart (1898 [1895]:204–205) and by Malloch (1915–17b:223–224), as stated under the discussion of the species.

The species of the genus Pilaria may be separated by the following keys:

Larvae

Ventral lobes of spiracular disk elongate, heavily marked with brownish black; coloration pale yellow. . . . . *P. tenuipes* (Say) (p. 873)
Ventral lobes of spiracular disk short, pale; coloration deep yellow. *P. recondita* (O. S.) (p. 874)

Pupae

1. Pronotal breathing horns short, black; lobules of cephalic crest blunt and rounded. *P. quadrata* (O. S.) (p. 875)
   Pronotal breathing horns elongate, pale, brownish yellow or yellow; lobules of cephalic crest elongate, finger-like. 2

2. Antennal sheaths of male elongate; pronotal breathing horns longer, pale yellow. *P. tenuipes* (Say) (p. 873)
Antennal sheaths of male short; pronotal breathing horns shorter, yellowish brown. *P. recondita* (O. S.) (p. 874)

Pilaria tenuipes (Say)

1823 *Limnobia tenuipes* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 21.
1869 *Limnophila tenuipes* O. S. Mon. Dipt. N. Amer., part 4, p. 210–211.

Pilaria tenuipes is a widely distributed crane-fly thruout eastern North America. The immature stages are commonly found in the mud of swamps, or near streams and other bodies of water. This is the unknown Limnophila described by Hart (1898 [1895]: 204–205), and also considered in much detail by Malloch (1915–17 b: 223–224), who found the pupae along the banks of the Sangamon River in Illinois.

Larva.— Length, 16 mm.
Diameter, 1.4–1.5 mm.

Coloration of living larva, pale brownish yellow. Body covered with a long, dark-colored, appressed pubescence, more conspicuous on posterior segments. Lateral pencils of setae near base and apex of segments. Antepenultimate segment of body capable of globular distention, covered with numerous transverse rows of microscopic roughened points. Spiracular disk (Plate XLVIII, 230) moderately large, surrounded by four lobes; ventral lobes long and slender, inner face with closely approximated, transverse, brownish black lines which cause entire face to appear dark; near tips of lobes these black marks tapering out into a long point; basal parts of dark marks subcontiguously hollowed out interiorly to form a large pale area below spiracles; ventral lobes fringed with long, pale hairs, some of them exceedingly elongate. Lateral lobes very small, blunt, tending to be reduced, bearing short fringes of dark hairs. Anal gills slender, pale in color.

Head capsule of Ulomorpha type and not very different from that of the type genus; dorsal plate broad basally, narrowed gradually behind to near tip where it expands into a very large spatula. Epipharyngeal region of labrum and maxillae fringed with dense tufts and brushes of long yellow hairs. Maxillary lobe relatively small but elongate, hyaline, tapering to flattened apex. Antenna (Plate XLVIII, 229) with basal segment elongate, bearing at its tip an elongate apical papilla which is a little longer than the segment, bluntly rounded at its tip, and delicately sculptured. Mandible (Plate XLVIII, 228) very long, hinged, at its base an acute tooth equal in length to about one-third length of mandible; in the type larva, the left mandible a little longer than the right mandible. Mental region not chitinized.

Pupa.— Length, 10–15 mm.
Width, d.-s., 1.5–1.6 mm.
Depth, d.-v., 1.6–1.8 mm.

Coloration dark brown; pronotal breathing horns light yellow, extreme bases brownish. Cephalic crest small, composed of three slender, finger-like lobes which are tipped with strong setae; on front, before crest, two setiferous lobes. Labrum small, bluntly rounded

at apex. Labial lobes oval. Maxillary palpi slender. Antenna of female moderately elongated, reaching to just beyond wing root. Pronotal breathing horns (Plate XLIX, 233) elongate, cylindrical, sinuous, transversely wrinkled, apex scarcely enlarged but deeply split on inner margin; a setiferous tubercle ventrad and laterad of breathing horns. Thorax with a very high anterior median crest. A slender, setiferous tubercle above wing axil, and two others on either side of median line. Sheaths of halteres long and slender. Leg sheaths ending about on a level, or those of hind legs the shortest and those of fore legs a little longer.

Abdominal segments divided into two annuli. Tergites (Plate XLIX, 235) on posterior ring with a caudal row of blunt, naked tubercles; at end of row two setae; on either side of median area and just in front of row, a large setiferous tubercle; at base of ring two naked tubercles, one on either side of median line; two slender setiferous tubercles near margin of ring. Basal ring with four naked tubercles. (The third pair of tubercles found in the pupa of *Pilaria quadrata* is vestigial.) Pleura with four tubercles, two on each ring, the basal one of each ring setiferous, the posterior one naked. Sternites with six naked tubercles on basal ring, arranged in three transverse pairs; on posterior ring at base two setiferous tubercles, each with two bristles, directly behind last naked tubercle of basal ring; at caudal margin two or three large tubercles near end of row and about four or five small naked tubercles between. Female cauda (Plate XLIX, 234 and 236) very elongate, tergal valves slightly upcurved, terminating in a sharp spine and with two setae on outer face. Eighth tergite with four elongate lobes; posterior pair blunt, directed laterad; anterior pair elongate, slender, with two setae laterad of each. A blunt lobe on pleural region. Pleura with three or four powerful tubercles, with a seta located between the more dorsal pair. Sternal region with four small setae, two on either side of broad median area.

Nepionotype.— Orono, Maine, July 1, 1913. No. 50-1913.
Neanotype.— With type larva.

Pilaria recondita (O. S.)

1869 *Limnophila recondita* O. S. Mon. Dipt. N. Amer., part 4, p. 212-213.

Pilaria recondita is a common crane-fly thruout the northeastern United States. The immature stages are swamp inhabitants, and are very frequently found in exactly the same situations as are those of *P. tenuipes*. *P. recondita* belongs to the same group as *P. tenuipes*, and the pupae of the two species are very difficult to distinguish.

Larva.— Length, 15 mm.
Diameter, 1.2 mm.

Color a uniform light yellow.

Body covered with a long, appressed, yellow pubescence and with a few long setae. Spiracular disk very small, in a position of rest almost closed, surrounded by four lobes; ventral lobes moderately elongated, fringed with long, golden-yellow hairs which are longest at tips of lobes; if bent backward these elongate hairs extending to beyond gills; inner face of lobes almost unmarked, with only a delicate brown line extending from tip toward base

for a distance equal to about one-half length of lobes; lateral lobes small, subdorsal in position, separated by a narrow notch, their inner faces opposed to each other, margin fringed with short, golden-yellow hairs. Anal gills four, moderately elongated.

Head capsule as in *P. tenuipes*. Antenna with sculptured apical papilla tapering to blunt tip; besides this papilla, an even longer, hyaline, flattened blade. Mandible with apical bladelike part shorter and stouter, with two subequal stout triangular teeth at base (Plate XLVIII, 227).

Pupa.— Very similar to pupa of *P. tenuipes*, but smaller. Antennal sheaths of male short. Breathing horns a little shorter than in *P. tenuipes* but still much longer than in *P. quadrata*, of a pale yellowish brown color. On abdominal tergites, along caudal margin of posterior ring, from four to seven naked tubercles between the setiferous tubercles (in *P. tenuipes*, four or five). Male cauda (Plate L, 237) with dorsal lobes stout, cylindrical, narrowed at tips, divergent, directed caudad and ventrad; on outer face before tip a slender seta; ventral lobes blunt, with a flattened ventral tubercle at base of notch. Segment 8 on dorsum with posterior lobes blunt, straight, directed caudad and slightly laterad, but not so strongly as in *P. tenuipes*.

Nepionotype.— Orono, Maine, July 3, 1913.
Neanotype.— Ithaca, New York, emerged June 11, 1917. No. 112–1917.
Paratypes.— Pupa, Orono, Maine, placed in rearing as a fully grown larva, June 26, 1913; emerged as an adult male, July 3, 1913, showing a pupal duration of seven days. Larva, Orono, Maine, July 5, 1913 (No. 74–913).

Pilaria quadrata (O. S.)

1859 *Limnophila quadrata* O. S. Proc. Acad. Nat. Sci. Phila., p. 241.

Pilaria quadrata is a widely distributed spring and early summer species. The immature stages are very similar to those of *P. tenuipes* and *P. recondita*. A pupa was found by Dr. Needham in the Indian Spring, Ithaca, New York, where it was found floating among the water cress. From this pupa an adult female fly was reared. On June 3, 1917, the writer found two fully matured male pupae in Chickaree Woods near Ithaca. There had been a very heavy rainstorm on the preceding day, and the low spots in the woods had been converted into small ponds, many of the insects that normally live in the mud or beneath the decaying leaves being forced to the surface. The pupae of *P. quadrata*, as well as an abundance of Tipula larvae, were found clinging to small islands of débris floating on these temporary woodland pools. The adult flies emerged on June 3.

Pupa.— Length of cast pupal skin, 9–12 mm.

Coloration almost black, including pronotal breathing horns; abdomen more dusky gray. Cephalic crest small, black, trilobed, each lobe with a seta at apex. Labrum narrow, blunt at tip. Labial lobes rounded. Sheaths of maxillary palpi elongate, tapering to the

slender points. Antenna short in both sexes. Pronotal breathing horns (Plate L, 238) moderately elongate, cylindrical, transversely wrinkled, at tips smooth, flattened, and slightly enlarged. A tubercle with two long setae above wing axil. Two setiferous punctures on dorsum on either side of median line. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending before tip of third abdominal segment, the tarsal sheaths ending about on a level or the hind legs shorter.

Abdominal segments with tergites (Plate L, 239) 2 to 6 provided with eight naked, discal tubercles, arranged in four transverse pairs, the third pair more approximated; laterad of third pair of naked tubercles, two small setiferous tubercles; on seventh segment one of the four pairs of tubercles lacking; near caudal margin of segments a transverse row of weak, setiferous tubercles; on either side of median line, in alinement with discal tubercles and just anterior to the transverse setiferous row, a large tubercle provided with three setae. Pleural region carinate, each segment armed with four slightly curved tubercles: anterior one solitary, setiferous; second one solitary, naked; third one with two or three setae; posterior one bifid, naked. Sternites (Plate L, 240) with six naked, discal tubercles corresponding to those of tergites but reduced in number. Subterminal armature weak, ends of rows tuberculate; an isolated setiferous tubercle ventrad and laterad of ends of rows. Male cauda (Plate L, 242) elongate; dorsal lobes elongate-cylindrical, directed caudad and slightly dorsad, tapering to acute tips; three weak setae on outer ventral face; ventral lobes blunt, much shorter than dorsal lobes, with a blunt median lobule between them at their base; eighth segment on tergum provided with a large, blunt, median tubercle, with two large posterior lobes which are directed caudad and with two tiny lobes on either side in front; sternum with a transverse row of four separated setiferous tubercles; caudal margin with a transverse row of about eight or nine pale tubercles on either side, the outermost the largest; a small seta above second tubercle at ends of row. Female cauda (Plate L, 241) very long and slender, subacicular, sternal valves a little shorter than tergal valves; tergal valves terminating in blunt cylindrical points.

Neanotype.— Male pupal skin, Ithaca, New York, June 3, 1917.
Paratypes.— Pupa, a male skin with type pupa; a female skin, Ithaca.

Subtribe **Hexatomaria**

The subtribe Hexatomaria comprises a well-defined division with but four known genera, three of which are North American and are considered in this paper. The only other group of crane-flies with which the species may be confused are certain of the Limnophilaria, especially the Ulomorpha group of genera.

The larvae have the labral sclerite of the head capsule large, separated from the remainder of the capsule by a distinct suture. The epipharyngeal region is restricted to the anterior median part of the sclerite, and is provided with two large tubercles on either side, which are tipped with two or three hyaline, cylindrical papillae. Between these papillae is a brush

of hairs surrounding two pairs of setiferous tubercles. The mental region is not chitinized. The dorsal plates of the head capsule are widely separated from each other by a median split.

The pupae are often armed with spines or tubercles on or about the head and the thorax. The lateral abdominal spiracles are large and functional.

The genera of the subtribe Hexatomaria may be separated by the following keys:

Larvae

1. Coloration of body a deep saturated orange-yellow; spiracular disk with ventral lobes unlined with darker, bearing at tips a few very long hairs... *Penthoptera* Schin. (p. 891)
   Coloration of body pale yellow, whitish, or greenish; spiracular disk with lobes lined with dark brown or black........2
2. Size small, form slender (length 14–15 mm., diameter 1–1.3 mm.).. *Hexatoma* Latr. (p. 877)
   Size larger, form stouter (length over 15 mm., diameter over 1.6 mm.) *Eriocera* Macq. (p. 881)

Pupae

1. Pronotal breathing horns short and stout, red at base and apex, the remaining part dark-colored, transversely wrinkled; horns bent strongly toward each other at tips. *Penthoptera* Schin. (p. 891)
   Pronotal breathing horns not as above........2
2. Size small (length under 10 mm.)........*Hexatoma* Latr. (p. 877)
   Size larger (length over 12 mm.)........*Eriocera* Macq. (p. 881)

Genus **Hexatoma** Latreille (Gr. *six* + *I cut*)

1809 *Hexatoma* Latr. Gen. Crust. et Ins., vol. 4, p. 260.
1818 *Nematocera* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 209.
1818 *Anisomera* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 210.

Larva.— Size small (length of *Hexatoma megacera* about 14 mm.). Spiracular disk surrounded by two pairs of lobes, ventral pair the longer, inner face marked with a narrow brown line which is expanded at its inner end. Head capsule with lateral angles of labrum elongate and densely clothed with hairs.

Pupa.— Size small (length under 10 mm.). A large spinous tubercle on scape of antenna. No median projection on mesonotal scutellum. Pronotal breathing horns short and straight. Wing pads with cell R_2 very small and M with but a single branch reaching wing margin.

The genus Hexatoma includes a small number of forms with a chiefly Holarctic distribution, there being about eleven Palearctic, two Ethiopian, and one North American species so far described. The adult flies of the North American species, *Hexatoma megacera*, are common on vegetation along the banks of rather large streams. They are discussed herein in detail under the account of this species. The adult flies of some of the larger European species have habits quite like those of the genus Eriocera,

as discussed elsewhere in this paper (page 705). Riedel (1909:29) describes in some detail the habits and swarming of *H. bicolor* (Meig.), the males of which are very active in the forenoon during the hours of brightest sunlight, the females resting on the willow branches near by. Similar habits are recorded by Riedel (1910:30) for *H. saxonum* (Lw.). The immature stages of the European species are practically unknown, the only original reference being that of Von Röser (1834), who states that the larvae of *H. nigra* Latr. live in the sand along the banks of streams.

Hexatoma megacera (O. S.)

1859 *Anisomera megacera* O. S. **Proc. Acad. Nat. Sci. Phila., p. 242.**

The adult flies of *Hexatoma megacera* are on the wing during the months of May and June and may be swept from the rank vegetation along the streams from which their larvae emerged. The following notes on copulation, resting positions, egg laying in nature and in captivity, and other details, are quoted from published field observations (Alexander, 1915 c: 143–145):

May 14, 1911 — This usually rare insect was common on a grassy plot of land along Cascadilla Creek [Ithaca, New York]. The flies sit on the blades of grass, the long antennae of the male directed straight ahead. The males are very poor fliers and prefer to drop to the ground when disturbed and clumsily work their way off along the ground. When approached from the side they are much more easily alarmed and fly away. When approached from above, they do not move until the stick, finger, or whatnot, is within a couple of inches, when they remove the fore feet from the support and, on nearer approach, fall to the ground. When in copulation, the female tries to disengage by rapidly vibrating the wings in attempted flight, repeating this often, from every one to five seconds until disengaged or exhausted. The male can disconnect himself at will. In copulation the female is always uppermost unless exhausted, when both sexes lie flat on a grass-blade. The female has the head up, the male the head downward; copulation always takes place on a vertical support, usually a blade of grass, sometimes a plant stem. The sexes remain in copulation for quite a long time and are perfectly motionless. All of the legs of both sexes are on the support unless in a position where this is physically impossible, in which case as many as possible are used; the hind legs of both sexes are held at right angles to the support, the forelegs in front. After copulation the female generally drops to the ground, the male, after a few moments' rest, flies away. Specimens in copulation were found in abundance from 2 to 4.30 p.m. when no more could be discovered. From 4.30 to 7 p.m. solitary males were common, but no females could be found on the grass-blades. At 4.30 p.m., a few females were found clinging to the trunks of the willow trees about two feet from the ground. At 5.30 p.m., females were noted in small groups over the water, evidently engaged in oviposition, as they frequently dipped down to the surface. These latter were in company with a large swarm of dancing empidid flies (Rhamphomyia). Of the great numbers that were picked from grasses in the afternoon a considerable proportion were females and toward 5 p.m. they commenced egg-laying on the sides of the containing vessel, large shell vials. By 7 p.m. the sides of the vials were black in places with the large, dark-colored eggs. This data would seem to place the time for oviposition at about sunset. The females are very good fliers and often travel for long

distances before alighting as is shown toward sunset when they fly for long stretches upstream. The males are rather poor fliers, due in part, possibly, to the weight of the long antennae and, as stated before, this sex prefers to skulk rather than fly. When the males fly, they do so heavily and seize the first support that they collide with and hang on, occasionally flying on immediately to another support. When the male comes in contact with a stem, he very often ascends to the top by means of a part-flying, part-climbing motion and, on reaching the summit, flies off to another place. As a rule the flies, especially the females, alight on a single grassblade, but very often the males are observed on two blades, the legs of one side on one blade and those of the opposite side on the other; when the body thus hangs between the stalks, the tarsi diverge from one another, whereas on a single support, the legs converge.

Hexatoma was preyed upon by large numbers of a scatophagid fly that occurred in great abundance in this vicinity and seemed to be subsisting almost entirely on these flies. At least twenty of these predaceous flies were noted with Hexatomae and this species seemed to constitute the principle insect enemy of the crane-fly. They would lurk on the grass blades and sally forth after their prey, carrying it back to some point to feed upon it. It is probable that the blood is taken since the body of the Hexatoma appeared almost uninjured when examined. On an old beam where males had a habit of walking up the vertical face, a small spider's web was found, in which eleven specimens were entangled, two being still alive; eight of these were males, the remaining three, females.

The males especially can walk up smooth surfaces, as glass, moving the legs alternately and awkwardly. The first pair taken were in copulation but in placing them in the vial they became disengaged and ran about in the container. After a short time they began to copulate in the tube.

May 15, 1911 — A pair were taken in copulation at 10 a.m.; at 8 p.m. they were still in coitu, but this is exceptional as most of the pairs disengage very readily. In the morning the species is very active and although the males do not fly far, they fly readily and it is difficult to pick them up by hand. The females are excellent fliers especially in the morning.

Several pairs were taken in copulation and each pair was isolated in a separate vial in order to ascertain the number of eggs per female. The clutch was determined by dissection. When the captive insects began to oviposit, the eggs shot out from the body, at first slowly, then more rapidly, one per second, later much slower again, the eggs being extruded one at a time. The total period of oviposition required seven minutes; at the end of sixty seconds, in the space between sixty and seventy seconds, eighteen eggs were laid, or 1.8 per second. Toward the end of egg-laying, the eggs appeared much more slowly, one in two seconds. The eggs are quite sticky or viscid and adhere to the glass. When the female is in danger of death, as when she falls into the water, she begins, at once, to deposit the egg-complement. In nature it seems probable that one egg is laid at each descent to the water. As soon as the female touches the water, although she has not deposited an egg all day, she immediately starts to deposit the oblong black eggs. After the last egg is expelled the muscles of the ovipositor still go through the motions of expulsion. One specimen was placed in the water and as usual began to deposit her eggs. She was decapitated, laid eleven eggs and tried to lay still more but failed. The number of eggs laid varied from 316 to 372 with an average of 347; the time required for oviposition varied from seven minutes to seven minutes and forty seconds. In most cases the number of the egg-complement is probably between 300 and 400.

The greater part of the larval existence is probably spent in the water, and it is only when the larvae are fully grown and ready to pupate that they come to land. On April 26, 1914, gravel from the bank of Cascadilla Creek was carefully examined, but no signs of larvae or pupae were to be discovered. On May 6, however, the same bank was examined and about ten larvae and seventy-five pupae were found. Sometimes the immature stages are very abundant. On May 12, 1917, near the place

just described, the writer found larvae and newly transformed pupae in great numbers, the former pupating in the dry sand rather distant from the water's edge. In one dry patch of sand on a rocky ledge, sixty specimens were found in six square inches of soil. The insects are often found in gravel or coarse sand that is thickly penetrated by grass roots and rhizomes, rarely in pure gravel. They are most commonly found in soil that has been recently deposited after freshets. The immature stages of Hexatoma are associated with larvae of *Eriocera spinosa, E. cinerea, Tipula bella,* and *Atherix* probably *variegata* Walk., with pupae of *Chrysops excitans* Walk., and with many beetles such as *Paederus littorarius* Grav., *Gastrolobium bicolor* (Grav.), *Bledius* sp., *Omophron* sp., *Dyschirius sphaericollis* Say, *Tachistodes partiarius* (Say), *Anadaptus discoideus* (Dej.), *Laccobius agilis* Rand, and other species characteristic of the sandy margins of large streams. The pupal duration of Hexatoma is six and one-half days.

Larva.— Length, 14–15 mm.
Diameter, 1–1.3 mm.

Color of body, pale brownish yellow.

Body covered with rather abundant appressed hairs, the subterminal distended part of abdomen with transverse rows of very short spines or setae, there being from thirty-five to forty such rows. Spiracular disk (Plate LI, 246) surrounded by four lobes; ventral lobes the longer, with a fringe of a few long hairs at apex; on inner face a long, narrow, brown mark, extending from the tip inward, the proximal end expanded; lateral lobes with numerous long hairs which are gradually shorter toward base of lobes. Spiracles circular, situated at base of lateral lobes; a dusky mark extending from spiracles dorsad.

Head capsule of usual hexatomine type, as described for *Eriocera longicornis* (page 888). Entire general features and details of mouth parts very similar to those of *Eriocera longicornis*. Labrum (Plate LI, 243) transversely oval, with frame strong and chitinized, anterior median part produced into a small lobe (Plate LII, 250) bearing two lateral papillae and two setiferous tubercles surrounded by short hairs; lateral margins of labrum produced into prominent lobes directed proximad and cephalad, densely hairy and entirely protecting anterior margin of labrum. Antenna (Plate LI, 244) with apical papillae shorter than segment, the largest papilla transversely sculptured (Plate LII, 251). Mandible (Plate LI, 245) long and slender, the lateral teeth more accentuated than in Eriocera; largest tooth with a flattened truncated blade in its axil, this in some cases broken up into two or three small blades; basad of largest lateral tooth a flattened lobe which is barely indicated in the species of Eriocera studied. Maxilla with outer flattened blade conspicuous; palpus near its base on inner side, similar to the condition obtaining in Eriocera; just laterad of palpus a powerful seta.

Pupa.— Length, 9.2–9.6 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.4 mm.

Pupa (Plate LI, 247) very similar to that of *Eriocera longicornis*, differing only in its small size, greater development of scapal spine, lack of projection on mesonotal prescutum, and a few lesser characters. Cephalic crest (Plate LI, 248 and 249) as viewed from beneath, very different in shape. Fore pair of legs much shorter than the others, ending just beyond posterior margin of second abdominal segment; hind pair of legs extending far beyond the others, ending beyond midlength of third abdominal segment; in some specimens the tarsal segments much closer to posterior margin of third abdominal segment, but usually a marked difference in tips of tarsi of the various legs. Cephalic crest as viewed from side, triangular, ending in an acute point directed strongly forward. Viewed from beneath, lobes conspicuously triangular, pointed, lying parallel or slightly divergent and separated by a deep median split. Spine on scape of antennae very large, conspicuous. Tubercle on labrum strongly developed. Antennal sheaths of male very long, those of female much shorter. Pronotal breathing horns short, straight. Mesonotum strongly wrinkled along median line; scutellar lobe not developed. Wing pads dark, venation not showing clearly but, if made out, the very short cell R_2 and the reduced *M* characteristic of Hexatoma alone. Posterior leg sheaths extending beyond level of middle legs, these, in turn, being longer than sheaths of fore legs.

Abdomen (Plate LII, 252) with about thirty-four spicules on sternite 4, about thirty in a straight, uninterrupted row on tergites 3 and 4, and about twenty on tergite 5. Chaetotaxy about as in *Eriocera longicornis*, but the seta lying ventrad of spiracle on pleurites much farther ventrad and very weak. Male cauda with sternal lobes strongly rounded, enlarged, and bent suddenly dorsad. Female cauda as that of male; ovipositor viewed from side with an obtuse notch; from beneath, sternite obtusely pointed and with a deep median split; from above, tergite almost flat across caudal margin, the lateral angles rounded, with a deep median split.

Nepionotype.— Ithaca, New York, May 6, 1914.
Neanotype.— Type locality, May 2, 1913.
Paratypes.— Several hundred larvae and pupae from type locality.

Genus **Eriocera** Macquart (Gr. *wool* + *horn*)

1830 *Caloptera* Guér. Voyage de la Coquille, Zool., Ins., pl. 20, fig. 2.
1838 *Eriocera* Macq. Dipt. Exot., vol. 1, p. 74.
1838 *Evanioptera* Guér. Voyage de la Coquille, Zool., vol. 2, part 2, p. 287.
1848 *Pterocosmus* Walk. List Dipt. Brit. Mus., vol. 1, p. 78.
1850 *Allarithmia* Loew. Bernstein und Bernsteinfauna, p. 38.
1857 *Oligomera* Dolesch. Natuurk. Tijdschr. Nederl. Indie, vol. 14, p. 387.
1859 *Arrhenica* O. S. Proc. Acad. Nat. Sci. Phila., p. 242.
1859 *Physecrania* Bigot. Ann. Soc. Ent. France, ser. 3, vol. 7, p. 123, pl. 3, fig. 1.
1912 *Androclosma* Enderlein. Zool. Jahrb., vol. 32, part 1, p. 34.
1916 *Globericera* Matsumura. Thous. Ins. Japan, add. 2, p. 471.

Larva.— Spiracular disk surrounded by four lobes which are rarely (as in *Eriocera cinerea*) subobsolete, inner face lined with brown or black, tips with fringes of moderately long hairs. Head capsule long, narrow, the constituent plates very slender; dorsal plate completely divided tho contiguous or approximated behind. Labral sclerite large and conspicuous, sensory tubercles and papillae crowded on median cephalic region. Mandible long, acute

at tip, with two teeth at about midlength. Maxilla with outer lobe greatly prolonged into a flattened blade. Antenna cylindrical or clavate, with three or four long papillae at tip. Mentum not chitinized, in *E. cinerea* with a flattened rectangular plate on either side, this armed with numerous hooks and spines.

Pupa.— Cephalic crest of various shapes and sizes, very reduced in *Eriocera spinosa.* Antennal sheaths of males of several species (*E. spinosa, E. longicornis, E. cinerea*) very long, extending beyond end of wing pad. Pronotal breathing horns of various shapes, acutely pointed in *E. spinosa*, short and blunt in several species. Head and thorax often with spines or tubercles on scape of antenna, on labrum, or (in *E. spinosa*) on face of eye; a tubercle on scutellum (in *E. longicornis*), one on dorsum of second abdominal segment (in *E. spinosa*). Abdominal segments with a conspicuous transverse armature of spines near posterior margin. Lateral spiracles large, distinct.

Eriocera is an extensive genus (including approximately 150 species) of medium-sized to large flies, most of which are tropical. The genus has not been found in Europe, but elsewhere it is represented by a host of species. The habits of the adult flies have already been noted (page 704). The immature stages are spent in sand or gravel near running water, more especially along large streams. A more complete account of the genus is given by Alexander and Lloyd (1914) and by Alexander (1915 c: 148–152).

The occurrence of the flies is somewhat local. During an entire summer of collecting in Maine in 1913, the writer did not find a single specimen of any species; and Dr. Dietz has stated that the only living individual which he has found was a single male of *Eriocera spinosa* taken in the Pocono Mountains in Pennsylvania. On the other hand, the flies are often found in countless numbers, and several species may be found associated together. Thus, at Ithaca, New York, in the sandy gravel along Cascadilla Creek, the immature stages of four species of Eriocera and one of the closely related Hexatoma occur together in unlimited numbers.

The species of Eriocera may be separated by the following keys:

Larvae

1. Lobes surrounding spiracular disk obsolete or nearly so; a flat, chitinized plate with serrate margins on either side of mental region. . . . . *E. cinerea* Alex. (p. 886)
   Spiracular disk surrounded by four slender lobes; no plate as described above on mental region. 2
2. Very large (length 40–45 mm., diameter 4–5 mm.); spiracular disk with ventral lobes narrowly lined with black, inner ends of each forked, Y-shaped; lateral lobes narrowly lined with black, inner ends of marks expanded. . . . . *E. spinosa* (O. S.) (p. 883)
   Smaller (length under 30 mm., diameter under 2.5 mm.); spiracular disk not marked as above. 3

3. Ventral lobes of spiracular disk bearing one or two very long, dark setae in addition to the shorter yellowish fringe; inner face of each lobe with a capillary black line which is suddenly expanded at its inner end into a triangular brown mark, the two marks inclosing an oval pale area between their proximal ends; lateral lobes with a capillary black line. . . . . *E. fultonensis* Alex. (p. 890)
   Ventral lobes of spiracular disk with apical fringe consisting of numerous long, pale setae; inner face of each lobe lined with pale brown, at about midlength gradually expanded into an elongate-triangular mark, the two marks inclosing a linear pale area between their proximal ends; lateral lobes with a brown line. . . . . *E. longicornis* (Walk.) (p. 888)

Pupae

1. Size large (length 25 mm. or over); pronotal breathing horns tapering to acute tips; cephalic crest small, reduced to four small tubercles; cell M_1 on wing pad present; a strong spinous tubercle on either side of median line at base of second abdominal tergite; a tubercle on eye. . . . . *E. spinosa* (O. S.) (p. 883)
   Size smaller (length under 18 mm.); pronotal breathing horns blunt at tips; cephalic crest prominent; cell M_1 on wing pad lacking; no tubercles on second abdominal tergite or on eye. 2
2. A tubercle on mesonotal scutellum. . . . . *E. longicornis* (Walk.) (p. 888)
   No tubercle on mesonotal scutellum. 3
3. Pleurites of abdominal segments with a transverse row of three setae ventrad and slightly caudad of spiracle; antennae of male elongated. . . . . *E. cinerea* Alex. (p. 886)
   Pleurites of abdominal segments with two stout setae dorsad and caudad of spiracle; antennae short in both sexes. . . . . *E. fultonensis* Alex. (p. 890)

Eriocera spinosa (O. S.)

1859 *Arrhenica spinosa* O. S. Proc. Acad. Nat. Sci. Phila., p. 244.
1869 *Eriocera spinosa* O. S. Mon. Dipt. N. Amer., part 4, p. 252–253.

Eriocera spinosa is the commonest of the large species of the genus in eastern North America. The larvae occur in great numbers beneath rocks in rapid water in the autumn, when they form a considerable proportion of the insect life in the streams. When about to pupate they go to the neighboring banks and live for some time in the sand or gravel. The habits of the larvae have been discussed by Alexander and Lloyd (1914:16–17) and by Alexander (1915c:149).

The larvae were found on May 1, 1913, along the banks of Fall Creek, Ithaca, New York, in considerable numbers. They were associated with young and mature pupae of *E. longicornis*, which were emerging in great numbers at the time. On May 27, both larvae and pupae of *E. spinosa* were found to be very abundant, the larvae being more numerous in the wetter places, the pupae in the drier spots. They occurred at various distances from the water's edge, from within a foot of the margin to as far back as eight or ten feet. The pupae are found in short, more or less vertical, burrows, from one to three inches below the surface. Not often

were larvae and pupae found in close proximity to each other. Pupae of *E. spinosa*, as well as of all other species of the tribe as known, are very active when removed from their burrows, wriggling rapidly to and fro, and are exceedingly tenacious of life. Larvae, as found on May 27, were mostly contracted; a few, however, were expanded and had the subterminal segment of the abdomen swollen. In this regard it may be mentioned that almost all of the larvae of crane-flies that live in the sand or mud along the banks of streams have this ability to inflate the end of the abdomen. Larvae of Eriopterini, of Pediciini, and of Hexatomini have been observed with this conspicuous enlargement. It is undoubtedly used to propel the larva thru the soil by alternate expansion and contraction of the segment.

Larvae of *E. spinosa* were placed in breeding jars on May 13 and adult flies emerged on the 28th. It is probable that the pupal stage is not longer than from ten to twelve days, at the most. On May 30 a large number of larvae and pupae were brought into the laboratory in a bucket of gravel. Some of the fully matured pupae transformed in the pail while being brought to the laboratory.

The larvae are carnivorous. Their powerful, sickle-shaped mandibles are capable of inflicting a painful bite on tender parts of the hand. S. G. Rich placed larvae in dishes together with the nymphs of various dragon flies. The smaller of the nymphs were eaten by the Eriocera larvae, thus confirming previous observations on the carnivorous habits of the species.

Larva.— Length when fully extended, 40–45 mm.
Diameter, 4–5 mm.

Color varying from very pale whitish to rather dark brown; in life, the skin showing conspicuous bronzy reflections.

Spiracular disk (Plate LIV, 262) surrounded by four slender elongate lobes, one pair being lateral, the other ventral, in position; inner face of lateral lobes with a capillary black line, this beginning as an enlarged black spot just ventrad of spiracle, reaching tip of lobe; dorsal outer edge of lobe with a dense fringe of long, conspicuous, reddish hairs, inner edge of row beginning just laterad of spiracle where the hairs are very short, gradually becoming longer to tip, where they are as long as the lobe itself; ventral lobe with a capillary black line on proximal edge, this dividing at base of lobe, the lower branch running along ventral margin of stigmal field and approaching its fellow of the opposite side on median line of body; a dense fringe of conspicuous reddish hairs at tip of lobe and continued on outer dorsal side for a short distance toward base; a few dusky brown spots on stigmal field between spiracles; two small hairs between spiracles. Spiracles rather small, widely separated. Underneath caudal lobes and behind penultimate swollen segment, four anal gills, short, stout, cylindrical.

the lateral pair directed outward, the inner pair directed caudad. Head capsule (Plate LIV, 267) broad in proportion to its length, measuring 3.5–3.8 mm. by 1.8–2 mm. (across dorsal plates). Papillae at tip of antenna short, not more than one-third length of segment. Mandible (Plate LIV, 271) lacking a prominent conical tooth at midlength, such as is found in *E. cinerea* and other species.

Pupa.— Length: male, 26.5–27 mm.; female, 25–28.5 mm.
Width, d.-s.: male, 3.4–3.9 mm.; female, 3.4–4 mm.
Depth, d.-v.: male, 4–4.2 mm.; female, 3.5–4 mm.

In life, pupae varying in color from very pale yellowish to dark brown or almost black, the deepest color being that of head and thorax of old pupae; body often showing bronzy reflections.

Cephalic crest very reduced, scarcely projecting beyond level of antennae; viewed from beneath, somewhat quadrate, the anterior lateral angles produced into small pointed lobes bearing a small seta at apex; viewed from side a second pair of lobes is seen, these being subequal to anterior lobes in size, and likewise setiferous. Spine of antennal scape very large, somewhat curved, directed ventrad. Inner caudal surface of eye with a conspicuous tubercle. Tentorial region produced into a small median tubercle. Tubercles at base of labrum very large, close together, their tips strongly chitinized; a small seta above each of these labral tubercles and another small seta on each cheek. Pronotal breathing horns long, slender, broad at base, flattened and rather pointed at tips, the organ arcuated so that apex is bent strongly ventrad. Mesonotal scutellar lobe (Plate LV, 280) prominent, rather strongly projecting. Wing pad light brown, venation showing very clearly, the presence of cell M_1 in connection with elongate antennae in male sex being found in this species alone in eastern North America. Leg sheaths with tarsal sheaths ending on a level, about opposite end of third abdominal segment.

Second abdominal tergite with a conspicuous basal tubercle on either side of median line. Abdominal segments (Plate LVI, 283) with subterminal rows of spines, there being about twenty to twenty-two on tergites 2 to 5; tergites 6 and 7 destitute of spines but with four subapical setiferous tubercles; tergites 2 to 7 with a conspicuous setiferous tubercle on ventro-cephalic angle of each posterior ring; eighth tergite concave on posterior margin, bearing a pair of strong apical tubercles on either side of median line. Pleural region of abdomen rather restricted, longitudinally wrinkled. Spiracles large, elliptical, transverse, placed about opposite midlength of segments. Three small setiferous tubercles ventrad and caudad of spiracle, and another similar tubercle on dorso-cephalic angle of each pleuron. Sternites on segment 3 with two spines on each outer angle; segments 4 to 6 with from sixteen to twenty spines; segment 7 with about ten spines; an isolated setiferous tubercle caudad and dorsad of ends of row; segments 4 to 7 with a setiferous tubercle about midlength of posterior ring; segment 8 lacking soft pleural region, bearing an apical row of strong spines which are interrupted only on dorsum and for a small space on median line of venter, there being about twenty of these spines in the circlet. Male cauda (Plate LV, 281 and 282) with ninth sternite rounded, swollen, with a deep median furrow bearing a small lobe on ventral side at end of split; ninth tergite produced caudad into two strong conical points separated by a V-shaped notch, these points directed caudad and slightly dorsad, each one a little split near tip on outer face and with a prominent lateral tooth at about midlength. Female cauda (Plate

LVI, 284) with ninth sternite elongated, cylindrical, its tip rounded, feebly split beneath; ninth tergite very long, pointed, with a deep median split.

Nepionotype.— Ithaca, New York, May 1, 1913.
Neanotype.— With type larva.
Paratypes.— Numerous larvae and pupae with types, May 1–15, 1913.

Eriocera cinerea Alex.

1912 *Eriocera cinerea* Alex. Psyche, vol. 19, p. 169–170, pl. 13, fig. 9.

Eriocera cinerea is locally common, flying in May. The larvae were found on May 16, 1917, in sand along the banks of Cascadilla Creek, Ithaca, New York. They have been found at various dates during the past few years, but always in scanty numbers. Larvae found on April 28 were associated with larvae of *Hexatoma megacera*, *Eriocera spinosa*, Atherix, and other insects. The larvae are stouter than those of *E. longicornis* and are pale whitish yellow, quite devoid of the greenish tints of the latter species. A larva found on April 28 transformed to an adult female on May 16. Additional larvae and pupae were found on May 24, and a few pupae on May 30, 1917.

The supposed larva of *E. longicornis* described by Alexander and Lloyd (1914:21–23) pertains to this species; the true *longicornis* is discussed later in this paper.

Larva.— Length, 15–16 mm.
Diameter, 2–2.2 mm.

Color light yellow.

Form almost terete, abdominal segments subdivided into two annuli. Subterminal abdominal segment greatly enlarged, capable of great distention. Spiracular disk (Plate LIV, 263 and 264) very reduced, the usual four lobes exceedingly small; ventral lobes practically obsolete, not projecting, each fringed with from twenty to thirty long, golden-yellow hairs; lateral lobes very short, triangular, fringed with from twelve to fifteen long hairs; a faint dusky mark from dorsal margin of each spiracle to edge of field; a faint vertical stripe between spiracles; ventral lobes marked with brownish black, the mark of each side three-pointed at its inner end, the innermost of these points connected with its fellow of the opposite side; lateral lobes with the marks elongate, triangular, the points directed outward. Spiracles small, oval, separated by a distance a little less than the diameter of one. Anal gills four, very short and inconspicuous.

Head capsule long and narrow, measuring about 1.5 by 0.275 mm.; dorsal plates of capsule with proximal anterior angles produced inward. Labral sclerite (Plate LII, 253) having labrum itself subquadrate. Mental region entirely lacking strongly chitinized points as in this group of genera. Present species showing a structure which is probably a part of labium, either mentum or hypopharynx, and which has not been found in any other species of the

genus (Plate LII, 254); this structure located on either side of capsule on ventral face, a flattened, subrectangular plate whose surface, except at base, is densely set with small spines and large pits; inner margin provided with large, acute spines, beginning at about one-third length of sclerite, gradually enlarged toward tip, at inner angle acute; these teeth interrupted before outer posterior angle, which terminates in a blunt, flattened lobe. Antenna cylindrical, apex obliquely truncated, terminating in a slender apical papilla which is longer than the segment that bears it, broad at base, tapering gradually to tip; two or three long apical setae; small auditory plates at about one-third length of segment. Mandible (Plate LII, 255) a powerful, slender, curved hook, at about midlength with a strong pointed tooth bearing in its axil a smaller tooth; as is usual in the genus, an egg-shaped chitinized piece isolated in one of the ventral tendons of mandible. Maxilla arising just ventrad of mandible, outer lobe persisting as a very elongate, bladelike organ.

Pupa.— Length, 13–15 mm.
Width, d.-s., 1.6 mm.
Depth, d.-v., 1.7 mm.

Head and appendages dark brown, thoracic dorsum a little paler; abdomen with posterior rings of tergum and sternum dark brown, producing a banded appearance.

Cephalic crest (Plate LIII, 257) very large and conspicuous, consisting of two rounded lobes behind, each tipped with a strong seta; anterior part of crest directed ventrad and consisting of two lobes, the larger bearing a strong seta on outer face; viewed from front, these anterior lobes separated by a very narrow, U-shaped, median notch; crest of female a little smaller. Two blunt tubercles on scapal segments of each antenna. Junction of clypeus and labrum with two tubercles, above and slightly laterad of each a strong seta. A strong seta on cheek below eye. Labrum broad, very obtusely rounded at tip. Labial lobes rectangular, widely separated. Maxillary palpi blunt at tips (Plate LIII, 258). Antenna of male elongate, exceeding wing and ending opposite base of last tarsal segment of hind leg. Pronotal breathing horns short, slender, cylindrical, scarcely longer than cephalic crest. Two long curved setae and a smaller straight seta laterad and ventrad of base of each breathing horn. Lateral angle of thorax with two setae; two long setae above wing axil (Plate LIII, 256). A strong seta on either side of mesonotum and a group of two small setae in front of each of these. Wing sheaths extending to base of third abdominal segment. Leg sheaths extending to base of fourth abdominal segment; tarsal sheaths ending about on a level, or those of fore legs considerably shorter.

Abdominal segments (Plate LIII, 259) divided into two subequal rings. Chaetotaxy as follows: pleura with a seta on dorsal margin of basal ring; a transverse row of three setae on posterior ring, lying ventrad and slightly caudad of spiracle (as in *E. spinosa*); tergum with basal ring unarmed, posterior ring with a subterminal row of sharp black spines; two long setae at each end of row and a few small setae at intervals along row; a solitary seta on basal lateral part of posterior ring; armature weaker on posterior segments, on segment 7 being reduced to four separated groups of setae, the outer groups with a single spine; sternum with basal ring unarmed, posterior ring with a subterminal transverse row of stout black spines with two long setae at each end of row and an isolated seta laterad and caudad of end of row; at base of ring on either side a group of two setae, the lateral one the smaller. Male cauda (Plate LIII, 260) with the sharp dorsal lobes directed dorsad, rather acute at tips, two

setae on outer face before tips; viewed from above, these setae seen to be separated by a deep U-shaped notch; eighth segment with a dorsal pentagon of five closely approximated lobes; just laterad of these a group of three setae, the posterior one long and slender, the anterior one short and stout; pleural region produced into a long lobe tipped with a slender seta; on sternum two small setae on either side. Female cauda (Plate LIII, 261) elongate, tergal valves very long and slender, two delicate setae on either side before tip and a stouter one at tip.

Nepionotype.— Ithaca, New York, April 28, 1917.
Neanotype.— Fall Creek, Ithaca, May 18, 1917
Paratypes.— Larvae and pupae with types.

Eriocera longicornis (Walk.)

1848 *Anisomera longicornis* Walk. List Dipt. Brit. Mus., vol. 1, p. 82.
1869 *Eriocera longicornis* O. S. Mon. Dipt. N. Amer., part 4, p. 253–254.

Eriocera longicornis is probably the commonest species of the genus in the eastern United States. The adult flies are sometimes very abundant, occurring in swarms in late afternoon and early evening in May, some of the swarms numbering thousands of individuals. At other times of the day, the flies may be found resting quietly on bushes. The larvae live in the sand near the water's edge. The pupal duration is seven days. The detailed life history of this species is given on pages 704 to 708.

Larva.— Length, 17–19 mm.
Diameter, 2–2.3 mm.

Color, greenish brown.

Body covered with a long, appressed, dark pubescence. Penultimate segment of abdomen capable of great distention and destitute of pubescence; last segment of body conspicuously narrowed. Spiracular disk (Plate LIV, 265) surrounded by four slender lobes, the ventral pair the longer, bearing at tip elongate hairs, some of which exceed the lobes in length; on lateral face at about midlength a small pencil of hairs; on ventral face one or two long setae; inner face of ventral lobes lined with pale brown, beginning as a narrow brown mark at tip, at about midlength gradually expanded into an elongate triangular mark, the two lines inclosing between their inner ends a pale linear mark; lateral lobes similar to ventral lobes, fringed with long yellow hairs which are longer than the lobes; inner face of lateral lobes lined with pale brown. Spiracles rather large, separated by a distance equal to about one and one-half diameter of one. Anal gills pale. A few setae in transverse alinement on last segment behind lateral lobes. Two pairs of short black setae behind gills.

Head capsule and mouth parts very similar to those of Hexatoma, dorsal plates of capsule separate from each other, not fused as in the Ulomorphae; inner margins of dorsal plates straight and parallel. Labral sclerite broadly transverse, narrowed at ends, lateral margins produced into long lobes which are densely tufted with short, golden-yellow hairs. Median lobe of epipharyngeal region projecting, provided with two large sensory papillae, one on either side, and a few other setiferous papillae near tip, surrounded by numerous hairs.

Antenna elongate, a little narrower at base, at tip with three or four hyaline, seta-like papillae which are of various diameters and shorter than the segment, the largest of these papillae delicately sculptured with transverse lines. Mandible acute, curved, at about midlength with a blunt, flattened tooth, this with a smaller similar tooth in its axil. Maxillary blade very long and slender, about half length of capsule.

Pupa.— Length: male, 13.2–15.2 mm.; female, 14–15.4 mm.
Width, d.-s.: male, 2.1–2.2 mm.; female, 1.8–1.9 mm.
Depth, d.-v.: male, 2.1–2.3 mm.; female, 2.2 mm.

Young pupae very pale; soft abdomen almost white; chitinized anterior part of body very pale brown. Older pupae much darker, the chitinized part becoming black with a bronzy reflection; abdomen very dark brownish gray; breathing horns dark brown on apical half.

Cephalic crest (Plate LV, 275) very prominent, elongate, tapering to the subacute tips; lobes with blunt tubercles behind, as well as four long setae on each lobe, three on dorsal margin and a longer one on lateral face at about midlength; viewed from in front, lobes separated by a broad, square or U-shaped notch; ventral part of crest produced forward between antennal bases as a depressed lobe bearing a stout seta on either side. Tubercle on antennal scape very prominent. A slightly smaller tubercle on either side of clypeus, with a small rounded knob cephalad of each. Labrum truncated. Labial lobes roughly diamond-shaped. Maxillary palpi very broad, rectangular, tips truncated. Antennal sheaths of male greatly elongated, enlarged at base; viewed from beneath, the swollen bases nearly contiguous on median line, just above and proximad of inner margin of eye, with scapal tubercle described above. Antenna of male exceeding wing pads, those of female ending just beyond wing base. Pronotal breathing horns short and stout, straight, transversely wrinkled, directed cephalad, dorsad, and laterad; when viewed from beneath, completely concealed by large cephalic crest. Thoracic notum convex; mesonotum transversely wrinkled (Plate LV, 277); median lobe of mesonotal scutellum projecting dorsad and caudad as a blunt point (Plate LV, 272). Two or three setae above wing axil. Lateral angles of thorax subacute, with a weak seta. Wing sheaths attaining end of second abdominal segment. Leg sheaths ending before caudal margin of third abdominal segment; tarsi of hind legs the longest, the two inner pairs ending about on a level (Plate LV, 273).

Abdominal segments (Plate LVI, 285) divided into a basal and a posterior ring; tergites on posterior ring with a subterminal transverse row of spines, these varying from about thirty-two on segment 3 to about fourteen on segment 7; these rows of spines interrupted on dorso-median line; at each end of row, three long setae, and two additional groups of setae interspersed along row; two setae on either side at anterior-lateral angle of ring; tergites on basal ring unarmed; sternites on posterior ring with a subterminal transverse row of from twenty-four to thirty-two spines, with two setae at each end of row; an isolated seta on caudo-lateral margin, close to pleura; a group of two approximated setae near base of posterior ring, on either side, about at level of spiracles. Sternites on basal ring unarmed; pleurites on basal ring with a solitary seta at about midlength, but slightly nearer dorsal margin; posterior ring with two setae dorso-caudad of spiracle, and a third seta ventrad of it. Male cauda (Plate LVI, 286) very blunt, much narrower than remainder of abdomen; ventral lobes very blunt; dorsal lobes short, stout, ending in sharp points directed dorsad, on outer face a long and a short seta; segment 8 with a dorsal trapezoid of four lobes, the posterior

pair the longer, each with two setae; anterior pair of lobes a little more widely separated; laterad of latter pair of lobes, a tubercle bearing three setae; a long, powerful seta on pleura; two setae on either side of median line of sternum. Female cauda (Plate LV, 274) similar, but ventral lobes more pointed, slightly exceeding level of dorsal lobes.

Nepionotype.— Ithaca, New York, April 18, 1917.
Neanotype.— Fall Creek, Ithaca, May 2, 1913.
Paratypes.— Several hundred larvae and pupae with types.

Eriocera fultonensis Alex.

1912 *Eriocera fultonensis* Alex. Psyche, vol. 19, p. 168–169, pl. 13, fig. 7.

Eriocera fultonensis is a rather common but usually local species thruout the northeastern United States. The larvae are found in the same situations as are described for the other species of the genus, in sand or gravel near the margins of usually large streams. On May 30, 1913, larvae were found in considerable numbers along the banks of Fall Creek, Ithaca, New York, where they occurred in company with numerous larvae and pupae of *E. spinosa*, a few large tabanid larvae, a small tabanid pupa, and the following beetle associates: Bembidion, Schizogenius, Tachys, Gastrolobium, and a few others. The pupal duration is seven days (from May 31 to June 6, 1913).

Larva.— Length, 18–26 mm.
Diameter, 2–2.3 mm.

Color, pale flesh yellow; anterior segments of body a little darker.

Body long and slender. Spiracular disk (Plate LIV, 266) with ventral lobes long and slender, lateral lobes shorter; ventral lobes at their tips with one or two very elongate blackish hairs which are from two to three times length of lobes; in addition to these the usual apical fringe of yellowish hairs not exceeding lobes; near base on outer side a small pencil of hairs; each ventral lobe with a very delicate capillary black line which expands abruptly at its inner end into a brown area, these two areas inclosing between their proximal ends a more or less oval pale area (in some specimens the inner ends completely encircling this pale area, while in others the brown lines are not continuous over the disk); lateral lobes shorter, similarly fringed with yellow hairs which are longer than lobes; inner face of lobes with a capillary black line. Spiracles rounded oval, widely separated.

Head capsule and mouth parts almost as in *Hexatoma megacera* and *Eriocera longicornis*, as already described; epipharyngeal region (Plate LIV, 268) produced into a hemispherical rounded lobe which is densely covered with fine hairs; two large papillae on either side near tip, between them a terminal tuft of long yellow hairs surrounding two long, slender, setiferous papillae. Antenna with sensory papillae at tip short, about one-third length of segment.

Pupa.— Length, 14–16 mm.
Width, d.-s., 1.8–2 mm.
Depth, d.-v., 2.5–2.7 mm.

Fully colored pupae dark brown; cephalic crest paler; pronotal breathing horns pale yellow, darkening into brown at tips; wing pads light yellow, with dark venation showing clearly; pleurites of abdomen of a darker brown than sternites or tergites.

Body somewhat similar to that of *E. longicornis*, but general form much stouter. Cephalic crest (Plate LVI, 287) prominent, tuberculate, consisting of four lobes, the posterior lobes somewhat the larger, on posterior and lateral faces with two stout setae; a stout seta on ventral face of anterior lobes. Scapal spine lacking. Clypeal tubercles large, blunt, with a small setiferous tubercle above each. Labrum bluntly rounded at apex. Labial lobes elongate, diamond-shaped, tips rather acute. Pronotal breathing horns rather long and slender, transversely wrinkled, longer than cephalic crest. Mesonotum (Plate LV, 279) more convex than in *E. longicornis*. Wing pads usually showing venation clearly on pale background; vein *r* connecting R_1 with R_{2+3} distinctive of this species, lack of cell M_1 separating this pupa from that of *E. spinosa* and *E. brachycera*. Legs sheaths ending about on a level, the hind tarsi a little longer than the two inner pairs.

Arrangement of setae on abdomen (Plate LVI, 288) about as in *E. longicornis*. Pleura with two stout setae dorsad and caudad of each spiracle, and a weak seta ventrad of spiracle and close to it; basal ring with a single pleural seta; spicules on caudal margin of posterior ring small and numerous, on intermediate segments about forty in number; seventh sternite with about four to six spines at each end of row, the broad median area devoid of spines. Female cauda (Plate LV, 276) with tergal valves exceeding the long sternal valves, scarcely directed dorsad (this condition may be compared with that in *E. longicornis*). Male cauda with abdomen bluntly rounded at tip.

Nepionotype.— Ithaca, New York, May 30, 1913.
Neanotype.— With type larva, June 6, 1913.
Paratypes.— Larvae and pupae with types.

Genus **Penthoptera** Schiner (Gr. *sorrow + wing*)

1863 *Penthoptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 220.

Larva.— Spiracular disk surrounded by four blunt lobes, the ventral pair a little the longer, inner face not marked with darker, at tip with one or more long setae. Head capsule about as in Eriocera. Coloration a deep saturated yellow.

Pupa.— Cephalic crest with lobes rounded, setiferous. No distinct tubercles or spines on head or thorax. Pronotal breathing horns short, stout, cylindrical, apex expanded into a flattened head, stem coarsely wrinkled, base enlarged. Abdominal armature weak. Spiracles not well developed.

Penthoptera is a small genus which includes four European and three American species, two of the latter occurring in tropical America. The eastern North American *Penthoptera albitarsis*, discussed below, has been considered in some detail by the author in another paper (Alexander, 1915c: 152–157).

Penthoptera albitarsis O. S.

1869 *Penthoptera albitarsis* O. S. Mon. Dipt. N. Amer., part 4, p. 257–258.

The larvae of *Penthoptera albitarsis* are usually not uncommon in rich organic mud in shaded places thruout the range of the species. Larvae of many sizes, some very small, others apparently almost fully grown, may be found at a single time. This would probably indicate that the species emerges at intervals thruout the summer, rather than that it is double-brooded.

Larva.— Length, 10–12 mm.
Diameter, 1–1.2 mm.

Color bright chestnut-yellow, anterior half of body richer- and deeper-colored; thoracic segments suffused with brown; skin with a silky, iridescent reflection.

Body provided with numerous long, appressed hairs. A few setae on body, the following being the most conspicuous: one on lateral dorsal margin of last segment, near base of lateral lobes; a series of four groups of one or two in each row across dorsal surface of the three thoracic segments at about midlength; a group of two or three long setae on sides near caudal margin of segments. Subterminal enlargement of abdomen with about twenty-five transverse rows of fine points.

Spiracular disk (Plate LVII, 292 and 293) with four blunt lobes; ventral lobes densely fringed with long, pale hairs, those toward ends of lobes longer; one or more elongate setae near tip of each ventral lobe, these being longer than lobes themselves; lateral lobes with a similar fringe of rather short, yellow hairs; spiracular disk almost free from dark markings, a pale brown line extending dorsad from each spiracle and an indistinct brownish line along ventral margin of lateral lobes. Spiracles circular. Anal gills four, pale. Head capsule rather broad, dorsal plate with inner anterior angles rounded. Labrum (Plate LVII, 289) almost as in *Eriocera spinosa*, the extreme cephalic epipharyngeal parts with the usual papillae and setiferous tubercles; lateral papillae bearing at their tips three or four slender pegs; between these papillae two pairs of setiferous tubercles, a basal larger pair and a more apical smaller pair. Mandible (Plate LVII, 291) a little more curved than is usual in this subtribe, inner margin with a double tooth at about midlength.

Pupa.— Length, 10–10.5 mm.
Width, d.-s., 1.4–1.5 mm.
Depth, d.-v., 1.5–1.6 mm.

Thorax dark brown, wing and leg sheaths paler; pronotal breathing horns dark brown, swollen bases and tips much paler, light orange; abdomen brownish yellow.

Cephalic crest consisting of two widely separated rounded lobes behind, each bearing two setae; anteriorly the crest appearing as a large depressed lobe between antennal bases, with a very large, stiff seta on either side. A powerful seta on each side of region of clypeus. A seta on genal region between eye and sheath of maxillary palpus. Labrum evenly rounded or a little truncated at apex. Labial lobes widely separated, roughly rounded or indistinctly pentagonal in outline. Maxillary palpi broad, ending bluntly beneath or just before antennal sheaths. Antennae ending just beyond wing root in female, considerably longer in male.

Pronotal breathing horns (Plate LVII, 294) short, stout, cylindrical, apex expanded into a flattened circular head, stem coarsely and transversely wrinkled, base enlarged; breathing horns widely separated at their bases, but bent proximad so as to be almost contiguous at their tips; two strong setae laterad of base of breathing horn and an additional one in front of it. Mesonotum transversely wrinkled, with a distinct carina anteriorly (Plate LVIII, 296). Two groups of two setae on either side of median line, with an additional solitary seta; two longer setae above wing axil. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending at from two-thirds length to opposite end of third abdominal segment; tarsal sheaths ending about on a level, or, in some specimens, the hind tarsi a little longer than the others (Plate LVIII, 297).

Abdomen indistinctly divided into a narrow basal ring and a broader posterior ring; basal ring further very indistinctly subdivided into two subequal annuli. Abdominal armature weak; on sternites a subterminal transverse row of delicate spines with two setiferous tubercles at each end of row; on posterior ring two setae on either side at about midlength; tergites with four groups of two or three setae near posterior margin and an additional group of two setae on lateral margin of posterior ring near base; pleural region with a stiff seta on extreme anterior part of basal ring. Spiracles distinct; a group of two setae caudad and slightly ventrad of each spiracle, with an additional solitary seta caudo-ventrad of these. Female cauda (Plate LVIII, 298) with tergal valves of ovipositor only a little longer than sternal valves, at tip ending in a short, rather blunt point directed dorsad; on outer face before tip a short, stiff seta; segment 8 on dorsum with a close trapezoid of four irregular lobes; two setiferous tubercles on dorsal and lateral part of eighth segment, the more dorsal of these with two setae, the lateral one with a single seta; sternum with four stout setae, of which two are lateral and two are median in position. Male cauda (Plate LVII, 295, and Plate LVIII, 299) with sternal valves short and blunt; tergal valves slender, ending in an acute point directed dorsad; a few short setae on outer face before tip.

Nepionotype.— Ithaca, New York, May 25, 1917.
Neanotype.— Bool's hillside, Ithaca, June 5, 1917.
Paratypes.— Abundant larvae and a few pupae with types.

Subtribe **Polymeraria**

Genus **Polymera** Wiedemann (Gr. *many* + *part*)

1821 *Polymera* Wied. Dipt. Exot., vol. 1, p. 40.

Polymera is a tropical American genus including fifteen described species, one of which, *Polymera georgiae* Alex., occurs in the southeastern United States. A single additional species, *P. magnifica* Meunier (1906: 385), has been described from the Baltic amber (Lower Oligocene). The only species concerning the ecology of which we have any record is *P. geniculata* Alex., which has been found living in crabholes beneath rocks in Porto Rico. In this connection the long-horned deinoceritine mosquitoes

which live in similar habitats should be considered. Howard, Dyar, and Knab (1915:213) say, in describing these mosquitoes:

> These crab-hole inhabiting species possess peculiarly developed antennae in order, as we suppose, to enable them to detect the approach of their crustacean host and fly out of the holes before being overwhelmed in the water in the bottom by the incursion of the crab, whose body must completely fill the entrance to the hole.

It is curious and suggestive that the males of Polymera should likewise possess elongated and very complicated antennae.

Tribe Pediciini

The Pediciini constitutes a small tribe which seems to be divisible into two well-marked subtribes, the more generalized Adelphomyaria indicating a relationship with the Hexatomini.

The larvae of the Pediciini have the labrum broad and the epipharynx usually feebly armed. The mentum is completely divided into two parts, each half with not more than four, usually three, teeth. The hypopharynx is labriform. The maxilla consists of two lobes, distinct and separate in the Adelphomyaria, more or less approximated or fused in the Pedicaria. The mandible is powerful, ending in a strong apical point; the cutting edge has about four teeth; there is a simple tuft of setae on the prosthecal region in the Dicranotae and in Pedicia. The head capsule is very elongate, massive, and compact, with the posterior incisions very shallow. In the Adelphomyaria the cauda is surrounded by four lobes which are fringed with exceedingly elongate hairs; in the Pedicaria there are two ventral caudal lobes, each tipped with a very few setae. The anal gills are four in number and are segmented, the terminal segment being more or less retractile. In the Pedicaria prolegs are developed on the abdominal segments of some of the genera.

All of the species of the tribe, so far as is known to the writer, are carnivorous in their larval state, which is spent in mud or earth close to water.

The two subtribes of the Pediciini may be separated as follows:

Larvae

Spiracular lobes four in number, fringed with very long, delicate hairs.
Adelphomyaria (p. 895)

Spiracular lobes two in number, ventral in position, each tipped with from six to eight setae.
Pedicaria (p. 899)

The most important literature on the tribe Pediciini is as follows:

Pedicia rivosa	General	Scheffer, in Rossi, 1848:9.
Pedicia rivosa	Larva, pupa, general	Beling, 1879:45–46.
Pedicia rivosa	General	Reuter, 1893.
Pedicia rivosa	General	Wesenberg-Lund, 1915:335.
Pedicia albivitta	Larva	Needham, 1903:285–286; 1905:8.
Tricyphona immaculata	Larva, general	Beling, 1879:47.
Tricyphona immaculata	Larva, pupa, general	De Meijere, 1916:195–196.
Tricyphona schineri	Larva, pupa, general	Beling, 1879:47.
Dicranota bimaculata	Larva, pupa, general	Miall, 1893.
Dicranota bimaculata	Larva, pupa	Grünberg, 1910:66–67. (Copy.)
Dicranota bimaculata	General	Wesenberg-Lund, 1915:342–343.
Dicranota bimaculata	Larva	Malloch, 1915–17 b:219–220. (Copy.)
Rhaphidolabis tenuipes	Larva, general	Needham, 1908 a:212–214.

Subtribe **Adelphomyaria**

The division Adelphomyaria, as known, includes but the single genus Adelphomyia Bergroth, a curious genus of small crane-flies which, in the general appearance of the adults, strongly suggest the hexatomine subtribe Limnophilaria. The immature stages have not been associated with the adult flies by rearing, and there is, of course, the possibility of a mistaken reference. The immature stages of the insect herein described are easily recognized, however, and, no matter to what group it belongs, it deserves subtribal rank under the Pediciini.

Genus **Adelphomyia** Bergroth (Gr. *brother* + *fly*)

1891 *Adelphomyia* Bergr. Mittheil. Naturf. Ges. Bern, 1890, p. 134.

Larva (supposition).— Body with pencils of stiff setae, producing a spiny appearance. Spiracular disk surrounded by four short lobes which are fringed with exceedingly elongate hairs. Spiracles large, separated by a distance less than the diameter of one. Head capsule long and massive, all the plates firmly united except behind. Mandible acutely pointed. Maxilla of two elongate separated lobes. Antenna two-segmented, the terminal segment with three small papillae. Hypopharynx labriform. Mentum completely divided, each half with four teeth, the middle pair on each side the largest (*minuta*, supposition) or the second from the inside the largest (*americana*, supposition).

Pupa (supposition).— Cephalic crest small, each lobe with three setiferous tubercles. Pronotal breathing horns moderate in length, broadly tipped with light yellow. Mesonotum unarmed. Wing sheaths extending beyond base of third abdominal segment. Leg sheaths extending to beyond base of fifth abdominal segment. Abdominal armature weak, especially on posterior segments.

Adelphomyia is a small genus of crane-flies, including but four European and three North American species, and a doubtful species from Africa. The

insects resemble tiny species of the genus Limnophila. The adult flies are not uncommon on rank herbage, especially ferns, in woods and usually near running water. As already stated, the immature stages have not been reared, but larvae found by the writer in Maine are referred with considerable confidence to *Adelphomyia americana* and *A. cayuga*, while larvae and pupae of another species taken at Ithaca, New York, seem to be those of *A. minuta*. The larvae show a curious combination of tribal characters. The general appearance and the structure of the spiracular disk are altogether those of one of the Hexatomini; but the head capsule and the details of the mouth parts indicate a relationship with the Pediciini that cannot be denied.

Adelphomyia minuta Alex. (supposition)

1911 *Adelphomyia minuta* Alex. Can. Ent., vol. 43, p. 287–288.

Adelphomyia minuta is a characteristic late spring species, common in boggy woods and on vegetation along rapid streams. Larvae and pupae which are referred to this species were sifted from organic mud taken on Bool's hillside, Ithaca, New York, thruout May and early June, 1917. The pupae referred to this species strongly resemble those of Dicranophragma but in reality are very different. The species is discussed herewith in the hope that it may be definitely recognized in the future.

Larva.— Length, 4.5–5 mm.; caudal fringe, 2 mm. additional.
Diameter, 0.4 mm.

Coloration, saturated yellow with a faint orange-brown tinge.

Form narrow, body tapering gradually to both ends, spiracular disk narrowed. Body clothed with a delicate appressed pubescence and numerous tufts of conspicuous stiff hairs which produce a spiny or bristly appearance; the more conspicuous of these tufts located on pleural region, there being three such rows on abdominal segments — one on basal ring, the second and largest at base of posterior ring, and the third just before posterior margin of segment and more ventral in position; only the large intermediate tuft present on thoracic segments, the small brush on anterior annulus of abdominal segments lacking. Spiracular disk (Plate LIX, 305) with four lobes; ventral pair not more than three times length of lateral pair; inner face of lobes margined with brown; at tip of ventral lobes a fringe of exceedingly elongate hairs, which are from one-third to nearly one-half length of entire body and about fifteen times length of lobes bearing them; a stiff sensory bristle located in black margin at tip of lobe; lateral lobes with fringe of hairs relatively much shorter, tho still long. Spiracles large, close together, separated by a distance less than diameter of one, the middle piece black, the ring pale yellow. Anal gills four, slender, hyaline, each subdivided by constrictions into four lobes which are gradually narrowed from the base outward, the last being cylindrical.

Head capsule very compact, lateral plates united with broad dorsal plate except for a short distance behind. Labrum (Plate LIX, 300) broadly transverse; cephalic margin truncate or very slightly concave; epipharyngeal region with about five transverse interrupted rows of setae. Mentum (Plate LIX, 302) of two entirely separated plates, each half with four teeth, those at the ends the smallest, the outermost tooth tending to be reduced, the two middle teeth of each side notably larger than the others; outside of mentum a thin plate, its inner proximal margins nearly contiguous at median line of body. Hypopharynx labriform, projecting beyond level of both labrum and mentum; outer lateral angles densely hairy, median posterior area with about eight small, hyaline spines. Antenna (Plate LIX, 301), in caustic-potash mounts, hyaline; basal segment elongate-cylindrical, bearing at its tip about two papillae as follows: a long, slightly curved, cylindrical papilla which is finely sculptured, and immediately proximad of this a slightly smaller second segment of the antenna, bearing near its tip three tiny papillae, an inner flattened subspatulate blade, and two longer cylindrical papillae; near base of this second antennal segment a long seta. Mandible (Plate LIX, 303) rather long and slender, apical point narrow; about four small lateral teeth near ventral cutting edge, the most basad of these acute; a large dorsal tooth on cutting edge and two very small acute teeth near base; on dorsal face of mandible two long setae, and two somewhat shorter setae near heel of mandible; about five or six stout setae at prosthecal region. Maxilla (Plate LIX, 304) consisting of two elongated lobes which are separate from each other, the outermost the longer, the pale rounded palpus terminal in position; inner lobe shorter, with three elongate setae, of which one is apical and the longest is sub-basal in position.

Pupa.— Length, 4.5–4.7 mm.
Depth, d.-v., 0.8 mm.

Color light yellowish brown, the thoracic dorsum paler; pronotal breathing horns dark brown, apical quarter abruptly light yellow; abdomen brown, lateral and posterior parts of each segment darker.

Cephalic crest small, each lobe with three small setiferous punctures on anterior face; ventrad of crest between antennal bases a prominent median lobe. Labrum broad; apex truncated, indistinctly bifid. Labial lobes large, with a deep U-shaped median notch behind. Maxillary palpi rather short and stout, ending before joint of fore legs (Plate LX, 307). Pronotal breathing horns moderately elongate, curved slightly laterad, strongly divergent, cylindrical, of uniform diameter thruout their length. Mesonotum not very gibbous (Plate LX, 306). Thorax with a high anterior median carina. Wing sheaths extending beyond base of third abdominal segment, the venation indistinct. Leg sheaths rather long, ending at about one-third length of fifth abdominal segment; hind legs much longer than the others, middle legs a very little longer than fore legs.

Abdominal segments indistinctly subdivided into two rings, a narrow anterior ring and a much broader posterior ring; abdominal armature very weak, lacking on segment 7; basal annulus on tergites and sternites with a number of small pits on sides, these sometimes sparse or lacking; posterior ring with a transverse row of numerous long, stout setae or delicate spines before margin. Spiracles weak, at base of posterior ring. Male cauda (Plate LX, 309 and 310) with sternal lobes elongate, contiguous except at extreme tips; tergal lobes terminating in very slender and acute curved points, directed caudad and dorsad; tergite

8 swollen, with four blunt lobes, the posterior pair large, with their posterior faces setiferous. Female cauda (Plate LX, 308) with sternal valves much shorter than tergal valves and rather blunt at tips; tergal valves broad at base, narrowed at tips, which terminate in acute black spines, situated on lateral margin before apex, the spines directed dorsad, laterad, and caudad.

The larvae were common near Ithaca, New York, from May 10 to June 5, 1917. The pupae are described from one male and two females washed from mud from Bool's hillside, at Ithaca, on June 11, 1917. A little later in June adult flies of this species were common at this location.

Adelphomyia americana Alex. (supposition)

1912 *Adelphomyia americana* Alex. Pomona Journ. Ent., vol. 4, p. 829–831.

Larvae that were rather common in the rich organic mud from the Standpipe Woods, Orono, Maine, from July 1 to 14, 1913, are referred with some doubt to *Adelphomyia americana*. They are unquestionably congeneric with the species last described (*A. minuta*, supposition) and with the form discussed in the following pages as *A. cayuga*. A short time after the larvae of these three species were obtained, the adult flies appeared in considerable numbers in the same situations and there seems to be but little doubt as to the reference. Associated with the larvae of this species in the organic mud were a few larvae of Penthoptera, Rhaphidolabis, and other species of crane-flies.

The larva of the present species averages larger than that of *A. minuta*, when fully grown measuring 5.5 millimeters in length. In coloration it is light yellow. The ventral lobes of the spiracular disk have the dark markings on their inner face much more extensive, the apical half being suffused with brown. The mouth parts are similar to those of *A. minuta* as described, but the outermost of the two large teeth of each half of the mentum is reduced in size so that only a single tooth is of conspicuous size.

(Described from larvae taken at Orono, Maine. No. 66–1913.)

Adelphomyia cayuga Alex. (supposition)

1912 *Adelphomyia cayuga* Alex. Pomona Journ. Ent., vol. 4, p. 831.

The supposed larva of *Adelphomyia cayuga* occurred with specimens of the preceding (*A. americana*, supposition) at Orono, Maine, from July 1 to 13, 1913. This is a smaller species than the preceding, measuring but 4 millimeters in length, and is much paler, the color being almost

white. The condition of the mental teeth is almost as in *A. americana*, but the outermost of the two large intermediate teeth is a little larger. The larvae were rather frequent in the mud beneath saturated moss.

(Described from larvae taken at Orono, Maine. Nos. 57– and 67–1913.)

Subtribe **Pedicaria**

The Pedicaria comprise a well-defined division of the tribe Pediciini, including two groups of genera — the more generalized Pediciae, with the genera Pedicia, Tricyphona, Ornithodes, and Rhaphidolabina, and the specialized Dicranotae, with the genera Dicranota, Rhaphidolabis, and probably Polyangaeus.

The genera of the Pedicaria may be divided in the main as follows:

Larvae

1. Abdomen without prolegs, but with raised welts on segments 4 to 7, these covered with a microscopic scurfiness. (Group *Pediciae*) 2
   Abdomen with conspicuous cylindrical prolegs on segments 3 to 7, these with circlets of conspicuous chitinized hooklets around their ends . . . . . Group *Dicranotae* (p. 906)
2. Abdominal segments 4 to 7 with raised welts on both dorsal and ventral surfaces; sides of hypopharynx not parallel, narrowed toward base . . . . . *Rhaphidolabina* Alex. (p. 901)
   Abdominal segments 4 to 7 with welts on ventral surface only; sides of hypopharynx subparallel 3
3. Size very large, when fully grown 40 mm. in length; mental plates without a small lateral tooth . . . . . *Pedicia* Latr. (p. 899)
   Size smaller, when fully grown under 30 mm. in length; mental plates with a small lateral tooth . . . . . *Tricyphona* Zett. (p. 903)

The writer is unable to separate the genera of the group Dicranotae with the material available, and is inclined to suspect the congenerousness of Rhaphidolabis with Dicranota. The characters given by Malloch (1915–17 b: 217) to separate the two genera do not hold at all in a series.

It is impossible also to key the pupae with the present knowledge of the group.

Group **Pediciae**

Genus **Pedicia** Latreille (Gr. *a field*)

1809 *Pedicia* Latr. Hist. Nat. Crust. et Ins., vol. 4, p. 255.
1916 *Daimiotipula* Matsumura. Thous. Ins. Japan, add. 2, p. 463.

Pedicia is a small genus including but six described species, one occurring in Europe, one in Japan, and four in North America. Of the last-named,

two are eastern and two are western in their distribution. They include the largest and most beautiful species of the Limnobiinae.

The European *Pedicia rivosa* (Linn.) was found by Beling (1879:45–46) living in brooks and springs, or in wet spots among saturated leaves and other débris, sometimes associated with the larvae of *Tipula lutescens* Fabr. The pupae live in cylindrical vertical burrows, clothed in the last larval skin, and are able to move up and down in these passages Pupation lasts from one to two weeks.

Needham (1903:285–286, and 1905:8) was the first to describe and figure the larva of the commonest eastern species, *Pedicia albivitta* Walk.

Pedicia albivitta Walk.

1848 *Pedicia albivitta* Walk. List Dipt. Brit. Mus., vol. 1, p. 37.

Pedicia albivitta is a beautiful fly, common and widely distributed thruout the northeastern United States and Canada. The adults are on the wing in midsummer, and a few individuals may usually be found in June. The much rarer and more local *P. contermina* Walk. is a vernal species, on the wing in May and early June.

The larvae of *P. albivitta* live in cold springs and beneath saturated moss at the edge of streams. The writer has never succeeded in rearing this species to the adult condition.

Larva.— Length, 40–44 mm.
Diameter, 5–5.5 mm.

Color dark grayish brown above, paler at sutures and on posterior half of body; paler beneath, more grayish.

Body covered with a short, appressed, dusky pubescence. Thoracic segments with a pencil of small setae on pleural region. Abdominal segments with a few delicate lateral setae on posterior ring, at about midlength of segments. Ventral creeping-welts on abdominal segments 4 to 7 completely divided on median line, the welts covered with a microscopic scurfiness. Spiracles (Plate LXI, 311) circular, separated by a distance about equal to diameter of one, situated on a slightly protuberant elevation. Spiracular lobes two, ventral in position, short, slender, each with about six setae at tip. Anal gills (Plate LXI, 315) short, stout at base, before tip a constriction cutting off the elongate conical terminal segment, which is partly telescopic within the next basal segment.

Head capsule (Plate LXI, 312) massive, elongate, as in this division. Labrum broadly transverse, lateral parts a little enlarged and projecting anteriorly into blunt lobes, with a long seta near inner margin; median region of labrum with two widely separated setae, just laterad of each of which is a small papilla. Epipharynx roughened into a narrow transverse band of small spines. Mentum completely divided, each half continuous with ventral plate

of same side; anterior margin of each half with three slender, flattened teeth, the middle one of which is slightly the shortest. Hypopharynx conspicuous, labriform; anterior margin with a deep notch to form distinct lobes at lateral angles, and with several rows of small chitinized tubercles. Antenna (Plate LXI, 313) small; basal segment elongated, slightly curved, a circular auditory plate near base, at tip with numerous papillae, two of which are very long, nearly as long as segment itself; in addition to these, three or four tiny cylindrical papillae. Mandible powerful; ventral cutting edge with a row of about four teeth which are successively enlarged from tip to base; basal tooth very broad and flat, with outer margin truncate or slightly concave; teeth on dorsal cutting edge indistinct; a pencil of moderately delicate setae on scrobal region of mandible, and another at prosthecal region. Maxilla elongate; outer lobe larger than inner lobe, chitinized, apex with a very flat circular palpus (Plate LXI, 314) which is provided with a few disklike papillae around margin and a few scattered sensory papillae over pale apex; inner lobe with a long, powerful seta on ventral face and smaller setae near tip.

Nepionotype.— Ithaca, New York, June 1, 1917.
Paratypes.— Larvae from type locality.

Genus **Rhaphidolabina** Alexander (Gr. diminutive of *Rhaphidolabis*)

1916 *Rhaphidolabina* Alex. Proc. Acad. Nat. Sci. Phila., p. 540–541.

Larva.— Body covered with an abundant, appressed pubescence and tufts of erect hairs which are more numerous on anterior end of body. Creeping-welts on dorsal and ventral surfaces of abdominal segments 4 to 7. Spiracular lobes two, moderately elongated, each with about six hairs at tip. Spiracles large. Anal gills four, long and diaphanous. Head capsule long and massive. Mandible powerful. Antenna short, with two elongate papillae. Hypopharynx labriform, anterior margin concave. Mentum completely divided, each half with three large teeth and a much smaller lateral tooth.

Pupa.— Labrum truncate. Pronotal breathing horns short-cylindrical or slightly flattened. Abdominal segments with circular areas of spicules on pleurites. Intermediate tergites with a broad transverse band of tiny spines.

The genus Rhaphidolabina includes only *R. flaveola*, a curious pallid fly of the northeastern United States, serving as a connecting link between Tricyphona on the one hand and the Dicranotae on the other. The adult flies are common on rank vegetation in cold woods. The immature stages are spent in rich organic earth in the same situations as are frequented by the adult flies.

Rhaphidolabina flaveola (O. S.)

1869 *Rhaphidolabis flaveola* O. S. Mon. Dipt. N. Amer., part 4, p. 288.

The writer has found the larvae of *Rhaphidolabina flaveola* in Maine and in New York. At Orono, Maine, larvae were numerous in the rich

organic mud of the Standpipe Woods. One large larva was placed in a watch crystal with a fully grown larva of *Adelphomyia cayuga* (supposition). It at once seized the latter in its mandibles at about the third abdominal segment, and carried it helplessly all around the dish, occasionally shaking it, quite as a terrier does a rat.

Larva.— Length, 9.8 mm.
Diameter, 0.8 mm.

Color, brown to orange-yellow on anterior segments of body, becoming darker on abdominal segments due to the increase of pubescence.

Body covered with an abundant, appressed pubescence. Form terete; body moderately elongated, gradually narrowed toward both ends. Abdominal segments 2 to 8 divided into a narrow basal ring and a much broader posterior ring; segments 4 to 7 with conspicuous dorsal and ventral welts, which are larger and more conspicuous on posterior segments; these welts occupying basal ring of segments, and bisected by a deep longitudinal median impression, their surface covered with microscopic points. Thoracic segments before mid-length with a transverse row of stiff, dark brown hairs grouped in tufts or pencils; these hairs occurring on abdominal segments also, but less prominent here and occupying posterior region of segments; pencils more numerous on ventral and pleural regions, much scantier on dorsal surface except on pronotum. On sides of last abdominal segment, between spiracles and spiracular lobes, several long setae arranged in a transverse row, lacking on mid-dorsal and ventral regions. Spiracular disk (Plate LXII, 321) reduced to two ventral lobes, as in this division, these lobes slightly united basally, not very elongate, blunt at their tips, which bear about six dark setae. The two spiracles large and conspicuous, entirely exposed on dorsum of last segment, separated by a distance a little less than diameter of one; middle piece of spiracles large, black; ring brownish yellow. Anal gills four, long and slender, nearly hyaline, divided into lobes by slight constrictions; posterior pair of lobes a little longer than anterior pair.

Head capsule elongate, flattened, massive, as in this tribe. Labrum conspicuous, exceeding mentum and hypopharynx, the anterior margin fringed with long hairs. Mentum (Plate LXII, 316) completely divided, each half with three subequal prominent teeth and an additional much smaller lateral tooth; middle tooth of each side a little broader. Hypopharynx (Plate LXII, 317) labriform, anterior margin deeply concave, roughened. Antenna (Plate LXII, 318) short, the segment short-cylindrical, a little enlarged toward truncated apex; at tip several papillae, of which two are exceedingly elongate, very slender, about twice length of basal segment. Mandible (Plate LXII, 319) powerful, ending in an acute point; ventral cutting edge with about four teeth, the basal one of which is the largest, subtruncate, the next outer tooth a large, flattened, acute blade, two or three smaller flattened teeth just before tip; dorsal cutting edge with about two small teeth. Maxilla (Plate LXII, 3_0 short and very stout, the outer lobe much longer than the slightly smaller inner lobe.

Pupa.— (The following notes are taken from the cast pupal skins of the bred specimens

Labrum truncate. Labial lobes ovate. Maxillary palpi short and stout, broadest jus beyond base, tips blunt (Plate LXII, 322). Antenna moderate in length, tapering gradu ally to tip. Pronotal breathing horn (Plate LXII, 323 and 324) short, cylindrical o

slightly flattened, with a row of circular breathing pores along margin of distal end, which is slightly enlarged. Wing sheaths short. Leg sheaths much longer.

Pleural region of abdominal segments with circular areas which are armed with abundant, short, straight or slightly arcuated, rows of spicules, there being from five to seven spicules in each row; under high magnification these appearing as flattened, scalelike tubercles, fringed with the spicules described above; dorsum of intermediate abdominal segments with a broad transverse band which is rather densely set with tiny, sharply curved spines; on posterior segments these rows lacking or much weaker; dorsal bands lying posterior to level of lateral areas. Male cauda (Plate LXII, 325) with dorsal plate rather small, each half indistinctly bilobed at tip; outer lobe minutely tuberculate and with a small seta; ventral lobes large, blunt at tips; eighth tergite on either side with a small tubercle bearing two setae.

Nepionotype.— Ithaca, New York, May 14, 1917.
Neanotype.— Ithaca, May 26, 1917. Cast pupal skin; larva placed in rearing May 14, 1917, emerged May 26, male.
Paratypes.— Larvae, with type larva. Pupae, taken as larvae May 27, 1917, placed in rearing, emerged June 7, 1917. No. 79 - 1917.

Genus **Tricyphona** Zetterstedt (Gr. *three + bend*)

1837 *Tricyphona* Zett. Isis von Oken, p. 65.
1856 *Amalopis* Hal. Ins. Brit., Dipt., vol. 3, p. 15.
1856 *Bophrosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 183.
1860 *Crunobia* Kol. Wien. Ent. Monatschr., vol. 4, p. 391.
1881 *Nasiterna* Wall. Ent. Tidskr., vol. 2, p. 179, 191.

Larva.— Body moderately elongate, with ventral transverse creeping-welts on basal annuli of abdominal segments 4 to 7. Spiracular lobes two, moderately elongate. Anal gills four, divided into two to four lobes by from one to three constrictions. Head capsule massive, elongate. Eyespots distinct. Mandible powerful, ending in an acute point and with about four lateral teeth. Maxilla stout, consisting of two distinct lobes, the slender inner lobe closely approximated to the larger outer lobe. Antenna small; basal segment cylindrical at tip, with two exceedingly long, hyaline papillae (possibly lacking in *T. immaculata*). Hypopharynx labriform, anterior margin concave, roughened. Mentum completely divided, anterior margin of each half with three large teeth.

Pupa.— Pronotal breathing horns short and stout, blunt, angles rounded. Abdominal segments with transverse bands of spicules on tergites and sternites, and circular areas on pleurites.

Tricyphona is the largest genus of the Pediciini, including more than fifty described species. Almost all of these species are found in the Holarctic region, but two or three are Antipodal. In the eastern United States, *Tricyphona inconstans* is the most widely distributed and apparently the commonest species. This species and certain others (as *T. paludicola* Alex.) are characteristic swamp inhabitants, but other species

occur along running streams (*T. vernalis* [O. S.]) or near cliffs (*T. auripennis* [O. S.]).

The immature stages of the known species are usually spent in moist earth. In Europe, *T. immaculata* (Meig.) was reared by Beling (1879: 47) from larvae taken beneath decaying vegetable mold in the bed of a dried-up woodland stream. Other specimens were found in old horse manure in beech woods. De Meijere (1916: 195–196) found the same species in decaying leaves and other vegetable matter in wet spots near the banks of streams. *T. schineri* (Kol.) was found on August 19 in a wet spot in beech woods, where the larvae were associated with pupae of *Pedicia rivosa* in damp earth beneath 'débris,' adults emerging on September 6 and 12 (Beling, 1879: 47). The only American species whose immature stages have been found is *T. inconstans*, described herein.

Tricyphona immaculata (Meig.), the genotype, as described by De Meijere in the paper cited above, differs from *T. inconstans* as herein described in the following points: The antenna bears a very short terminal papilla instead of the two very long ones in the local species. The small lateral tooth on the mentum is not mentioned nor figured as appearing in *T. immaculata*. The anal gills are short and with but a single constriction. The pupa has the pronotal breathing horns small, kidney-shaped, the outer margin rounded. The fore legs are a little shorter than the middle legs, and these in turn are somewhat shorter than the posterior legs. The skin of the abdomen is very delicate, with crossrows of very small spicules, arranged in numerous irregular transverse rows, at the posterior margins of the segments, about seven such crossrows being present.

Tricyphona inconstans (O. S.)

1859 *Amalopis inconstans* O. S. Proc. Acad. Nat. Sci. Phila., p. 247.

Tricyphona inconstans is an abundant species thruout eastern North America. It has been recorded also from Europe, but the latter records are almost certainly erroneous. The writer found larvae of this species in rich mud at Larch Meadows, near Ithaca, New York, on May 15, 1917, in association with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, and *P. inornata*. Adults emerged on May 27, 1917 (No. 52-1917). An account of the association in which these larvae occurred

is given in connection with the discussion of *Rhamphidia mainensis* (page 831).

Larva.— Length, 17–17.5 mm.
Diameter, 1.3 mm.

Color pale yellowish white; anterior parts of body sometimes a more saturated yellow. Form moderately stout, body a little narrowed toward ends; surface of body almost glabrous, the vestiture being a microscopic pale pubescence and scanty scattered hairs. Ventral surface of abdominal segments 4 to 7 with a prominent transverse welt, which is hollowed out medially so as to appear as paired prolegs, these being unarmed with hooks or points. Spiracular lobes short, divergent, tapering gradually to the blunt tips, which are provided with seven or eight setae. Spiracles (Plate LXIII, 330) on a transverse oval elevation, small, rounded, separated by a distance greater than diameter of one; middle piece of spiracles large, black, rings narrow. Anal gills four, very long and slender, constricted into about four lobes which are successively narrowed from the base outward, the terminal division very slender.

Head capsule of the usual elongate, massive type of this tribe. Labrum large, projecting beyond hypopharynx, anterior margin with long hairs. Mentum (Plate LXIII, 326) large, completely divided, each half with three subequal narrow teeth and an additional reduced lateral tooth; on proximal margin of each half of mentum, near base of innermost tooth, a few tiny notches dovetailing into those of opposite half. Hypopharynx (Plate LXIII, 327) projecting far beyond mentum, labriform; anterior margin deeply concave and provided with small rounded papillae; lateral angles smooth, rounded, subchitinized. Antenna (Plate LXIII, 328) small; basal segment cylindrical, bearing at its tip two elongate papillae which are about one-half longer than basal segment alone; besides these an oval papilla. Mandible (Plate LXIII, 329) of the usual pediciine type, powerful, the apex running out in a long, curved point; ventral cutting edge very flat, cut into about five teeth, the two basal of which are very large; the most basal of these teeth squarely truncated, the left mandible with an additional small tooth on lower inner angle of this blade; the next outer tooth rather acute; outermost teeth small and flattened; dorsal cutting edge, as usual with this division, with two very small teeth located far out on apical point; a tuft of a few long setae on back of mandible near heel. Maxilla (Plate LXIII, 329) powerful, as in this group of genera, but not ex-erted from the prothoracic orifice when head is retracted; outer lobe very stout, feebly chitinized basally, hyaline at apex, which bears the flattened, disklike palpus; inner lobe slenderer, shorter, with a few setae and small papillae.

Pupa.— (The following notes are taken from the cast skins of the reared specimens.) Labrum with apex broadly triangular. Labial lobes large, ovate, tips narrowed and bluntly rounded (Plate LXIII, 331). Pronotal breathing horns (Plate LXIII, 332 and 333) very short, stout, roughly cylindrical, the apices truncated; in lateral outline, pentagonal, with a row of breathing pores around margin of truncate apex. Thoracic dorsum transversely roughened by short, irregular grooves.

Abdominal sternites with broad transverse bands of spicules on segments 5 to 7, the last of these three bands the weakest; similar bands on tergites 4 and 5, these bands subequal in size; pleural region with a large, roughly circular area of short rows of microscopic spicules,

these areas near base of segments. Female cauda (Plate LXIII, 334) with tergal valves elongate, tapering gradually to the rather blunt tips; sternal valves very small, blunt at tips; at base, on dorsal side of eighth segment, two setiferous tubercles.

Nepionotype.— Larch Meadows, Ithaca, New York, May 15, 1917. No. 52-1917.
Neanotype.— Ithaca, May 27, 1917, a cast pupal skin.

Group Dicranotae

Genus **Dicranota** Zetterstedt (Gr. *a fork*)

1838 *Dicranota* Zett. Ins. Lapponica, Dipt., p. 851, no. 164.

Dicranota is a small genus of crane-flies (about fifteen described species) occurring thruout the Holarctic region. Four species are found in eastern North America. None of the American species have been reared. In Europe, the life history and morphology of *Dicranota bimaculata* (Schum.) has been discussed in detail by Miall (1893) and by Wesenberg-Lund (1915:342–343). Larvae were found by Miall in numbers in the muddy banks of small streams and ponds, where they bury themselves in the mud and gravel. They creep about with ease and rapidity between the sand and gravel, and are able to swim well by a looping movement. Their food consists largely of small worms, *Tubifex rivulorum* Lam., which abound in these haunts. The pupal stage is passed in damp earth. The larva is stated to be about 18 millimeters in length, but this seems to be a maximum figure. The body is dirty white in color and is covered with fine, appressed hairs. Abdominal segments 3 to 7 bear paired retractile pseudopods, which are circled with three rows of chitinized hooks gradually decreasing in size from the tips inward. The anal gills, four in number, are distinctly segmented. The head capsule is elongate and massive, as in the tribe. The mentum is completely divided, its anterior margin having the usual six teeth. The mandible is of the usual pediciine type, with acute teeth on the ventral cutting edge and a brush of hairs near the prosthecal region. (Plate LXIV.)

The pupa is small, only about 10 millimeters in length, and has the pronotal breathing horns expanded and flattened at the tips. The dorsal surface of the abdomen is provided with roughened plates armed with rather strong and dense spines, there being one such plate on the third segment, two on the fourth to sixth segments, and one on the seventh segment.

Genus **Rhaphidolabis** Osten Sacken (Gr. *needle + forceps*)

1869 *Rhaphidolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 284–287.
1911 *Claduroides* Brun. Rec. Indian Mus., vol. 6, p. 288.

Rhaphidolabis is a small genus, including about fifteen described species ranging thruout the North Temperate Zone. The larvae strongly resemble those of Dicranota, and the two genera are undoubtedly very closely related.

Rhaphidolabis tenuipes O. S.

1869 *Rhaphidolabis tenuipes* O. S. Mon. Dipt. N. Amer., part 4, p. 287.

Needham (1908a:212–214) found adult flies of the species *Rhaphidolabis tenuipes* in great numbers in tent traps set over Beaver Meadow Brook in the Adirondacks in July and August, 1907. Larvae that almost certainly belong here were found among the rounded stones in the creek bottom.

Larva.— Length excluding caudal lobes, 8–9 mm.
Length of caudal lobes, 1 mm.

Abdominal segments 3 to 7 with prominent fleshy prolongations on ventral surface, these being retractile, unpaired, and widely separated on mid-ventral line, and bearing at tip a circlet of outcurved hooklets, with series of smaller hooklets beyond. Spiracular disk with the two ventral lobes long and obtuse at tips. (Further details are given by Needham.)

Rhaphidolabis cayuga Alex. (supposition)

1916 *Rhaphidolabis cayuga* Alex. Proc. Acad. Nat. Sci. Phila., p. 543–544.

Larvae which the writer refers to this species were found in Needham's Glen, Ithaca, New York, on March 30, 1916. Later in the season, in April and May, adult flies of the species are very numerous in this glen, and these account for the specific reference.

Larva.— Agreeing very closely with descriptions of both Dicranota and *Rhaphidolabis tenuipes*. Spiracles large, lying in a distinct longitudinal groove, by the closing of which they are capable of being entirely hidden. Antenna long and slender, tapering to apex, which bears numerous short papillae. Mandible with third lateral tooth of ventral cutting row very long and acute, much exceeding second tooth; basal tooth shaped like a pruning knife, with the cutting edge sinuate; at prostheeal region of mandible, a small tuft of about seven or eight long setae. Maxilla having the two lobes firmly united except on apical quarter.

Tribe Eriopterini

The tribe Eriopterini comprises a vast assemblage of usually small crane-flies whose geographical range is coextensive with that of the family.

The larvae, so far as known, are herbivorous. They show a remarkable uniformity in the structure of the head capsule. In the generalized members such as Molophilus and some Erioptera, the ventral bars of the head capsule are toothed at their anterior ends and form mental plates which are apparently homologous with those of the Pediciini. In Chionea an apparently similar condition exists, to judge from Brauer's figures. In the majority of species, however, the ventral bars of the capsule are not enlarged nor toothed anteriorly and do not function as the mental plates. The hypopharynx is preserved as a hemispherical cushion which is densely provided with setae. The mandibles are small and are blunt at their tips; the teeth of the cutting edge are usually three in number and blunt, but in some species (Ormosia, Gonomyia) they are longer and more prominent. A distinct prosthecal lobe or hook is usually developed, and near the base of the mandible is a slitlike opening bearing a fringe of long, yellow setae. The maxillae are rather large, hairy lobes. The labrum and epipharynx is long and narrow, and densely hairy. The antennae are remarkably uniform thruout the group, consisting of a stout cylindrical basal segment with a slightly smaller apical papilla of an elongate-oval shape. In the Elephantomyaria the condition is somewhat similar, the mandibles being very small, and the esophageal region being conspicuously grooved with parallel lines and ridges. The spiracular disk is obliquely truncated and indistinctly lobed in Chionea and Teucholabis; surrounded by four lobes in Elephantomyia; squarely truncated and surrounded by four (in Rhabdomastix) or usually five lobes. In the undetermined Eriopterine No. 1, the five lobes are spatulate flattened blades with the margins hooked. Anal gills are usually present and variously developed in the different genera. The pupa is rather slender, in the Elephantomyaria with the rostral sheath very long and the palpi strongly recurved. The head usually bears a small setiferous crest which is rarely lacking. The pronotal breathing horns vary considerably in form and relative size, being flattened into fans in some Gonomyia, small and trumpet-shaped in other Gonomyia and in Gnophomyia, elongate in most species. The mesonotum is usually armed at the crest with spines, hooks, or setiferous tubercles. The leg sheaths are very short in Gno-

phomyia but are longer in other genera, and the middle tarsi are usually shorter than the other legs. The abdominal segments are subdivided into two rings, the posterior ring with a transverse row of spines and setae before the margin. The lateral spiracles are small, protuberant, and, in some cases at least, apparently functional. The dorsum of the eighth abdominal segment is provided with four or five lobes, which are in some cases (as in some Ormosia) spinous at the tips.

The writer has subdivided the tribe Eriopterini into two divisions: the Elephantomyaria, with Elephantomyia and presumably Toxorhina and Ceratocheilus, and the Eriopteraria, including the other Nearctic genera as known. It is probable that Cladura and its relatives will require a division when their immature stages are better known.

The genera of the tribe Eriopterini may be separated by the following keys:

Larvae

1. Spiracular disk surrounded by four lobes....................2
   Spiracular disk not as above....................3
2. Ventral lobes with a single powerful seta; coloration a saturated golden yellow; lives under bark....................*Elephantomyia* O. S. (p. 952)
   Ventral lobes fringed with short setae; coloration pale yellow; lives in earth. *Rhabdomastix* Sk. (p. 942)
3. Spiracular disk obliquely truncated, appearing indistinctly trilobed or without lobes...4
   Spiracular disk squarely truncated, surrounded by five lobes....................5
4. Mandibles with eight teeth; mental plates with seven teeth; lives in earth. *Chionea* Dalman (p. 950)
   Mandibles with less than eight teeth; mental plates not toothed; lives under bark. *Teucholabis* O. S. (p. 945)
5. Spiracular disk ending in five flattened black plates which are finely toothed along their margins....................*Genus incertus*, Eriopterine No. 1 (p. 956)
   Spiracular disk not as above....................6
6. Ventral plates of head capsule expanded and toothed at anterior ends....................7
   Ventral plates not toothed as above....................8
7. Ventral plates with four teeth; coloration yellow; spiracular disk large, very heavily marked with black....................*Molophilus* Curt. (p. 911)
   Ventral plates with five to eight teeth; coloration green; spiracular disk very reduced, almost unmarked....................*Erioptera* (*chlorophylla* O. S.) (p. 918)
8. Marks of all the lobes solidly black....................*Trimicra* O. S. (p. 932)
   Some *Ormosia* Rond. (p. 922)
   Some of the marks more or less split by a pale line....................9
9. The three dorsal lobes solidly dark, the ventral pair split by a pale line....................10
   All paired lobes split by a pale line....................11
10. Coloration saturated yellow; anal gills bluntly rounded; lives under bark. *Gnophomyia* O. S. (p. 934)
    Coloration pale yellow; anal gills elongate; lives in earth. *Helobia* St. Farg. et Serv. (p. 928)
11. Lobes surrounding disk very stout, blunt; marks of lateral lobes surrounding spiracles and often suffusing disk.......*Gonomyia* Meig., subgenus *Leiponeura* Skuse (p. 939)
    Lobes surrounding disk longer; marks of lobes not so extensive....................12

12. All the lobes with two lines 13
    Dorsal lobe solidly dark .... Some *Ormosia* Rond. (p. 922)
13. No dark marks on disk between spiracles .... Some *Ormosia* Rond. (p. 922)
    Dark marks between spiracles 14
14. Spiracular disk very small; two spots on disk ... *Erioptera* (*megophthalma* Alex.) (p. 915)
    Spiracular disk large; four or six spots on disk .... *Helobia* St. Farg. et Serv. (p. 928)

Pupae

1. Rostral sheath very elongated; antennal sheaths lying across face of eye.
   Elephantomyia O. S. (p. 952)
   Rostral sheath not elongated; antennal sheaths lying behind eyes 2
2. Leg sheaths very short, barely exceeding wings; crest of mesonotum smooth or nearly so.
   Gnophomyia O. S. (p. 934)
   Leg sheaths longer, ending about one segment beyond end of wings; crest of mesonotum with spines or tubercles 3
3. Mesonotum at crest with numerous sharp spines; hind tarsi the longest, middle tarsi the shortest, fore tarsi intermediate in length .... *Helobia* St. Farg. et Serv. (p. 928)
   Mesonotum and tarsal arrangement not as above 4
4. Mesonotum at crest with six to eight tubercles provided with numerous setae; breathing horns fanlike or trumpet-like .... *Gonomyia* Meig. (p. 938)
   Mesonotum and breathing horns not as above 5
5. Mesonotum at crest with four sharp spines or two plates produced into spines 6
   Mesonotum at crest without distinct prominent spines 8
6. Mesonotum at crest with four spines 7
   Mesonotum at crest with a plate on either side split at tip into three or four teeth.
   Ormosia (*nubila* [O. S.]) (p. 923)
7. Crest of mesonotum with two large spines; pronotal breathing horns small, closely applied to thorax; lives under bark .... *Teucholabis* O. S. (p. 945)
   Crest of mesonotum with four large spines; pronotal breathing horns long, slender, curved; lives in earth .... *Molophilus* Curt. (p. 911)
8. Abdominal pleurites with a transverse subterminal row of from eight to twelve spines or stout setae; dorsum of segment 8 with a pentagon of five lobes.
   Ormosia Rond. (p. 922)
   Abdominal pleurites without such a row of spines or setae; dorsum of segment 8 with four or fewer lobes .... *Erioptera* Meig. (p. 914)

The most important literature on the tribe Eriopterini is as follows:

Molophilus bifilatus	Larva, general	Keilin, 1913: 4. (Hypodermal glands.)
Molophilus obscurus	General	Beling, 1879: 56.
Molophilus ochraceus	Larva, pupa	Beling, 1886: 193–194.
Erioptera maculata	Pupa	Beling, 1879: 49.
Erioptera flavescens	Larva	Beling, 1879: 50.
Erioptera lutea	Larva, pupa	Beling, 1886: 192–193.
Erioptera sordida	General	Beling, 1879: 56.
Cheilotrichia imbuta	General	De Meijere, 1920: 76.
Lipsothrix icterica	Larva, pupa	Beling, 1886: 192.
Ormosia haemorrhoidalis	Pupa	Beling, 1879: 48–49.
Ormosia haemorrhoidalis	Larva, pupa	Beling, 1886: 191–192.
Ormosia lineata	General	Beling, 1886: 202.
Ormosia nodulosa	General	Beling, 1886: 202.
Ormosia nodulosa	General	Cameron, 1917: 65.
Ormosia varia	Larva, pupa	De Meijere, 1916: 201–204.

Helobia hybrida	Larva, pupa	Beling, 1879:50–51.
Helobia hybrida	Larva	Hart, 1898 [1895]:199–200.
Helobia hybrida	Larva, pupa	Malloch, 1915–17b:229–230.
Trimicra pilipes	Larva, general	Gerbig, 1913:161–163.
Gnophomyia rufa	Larva, pupa	Hudson, 1920:32–33.
Gnophomyia tripudians	General	Gamkrelidze, 1913, a and b.
Gnophomyia tripudians	General	Keilin, 1913:3. (Hypodermal glands.)
Gnophomyia tripudians	Larva	Keilin, 1913:4. (Hypodermal glands.)
Gnophomyia tripudians	General	Edwards, 1919 b.
Gnophomyia tristissima	Larva, pupa, general	Malloch, 1915–17b:230–231.
Gonomyia tenella	General	Beling, 1879:56.
Rhabdomastix schistacea	Larva, pupa	Beling, 1886:195.
Trentepohlia bromeliadicola	Larva, pupa, general	Picado, 1913:356–357.
Trentepohlia leucoxena	General	Alexander, 1915 b.
Trentepohlia pennipes	Larva, pupa, general	De Meijere, 1911:50–51.
Teucholabis complexa	General	Johnson, 1900.
Chionea araneoides	Larva, general	Brauer, Egger, and Frauenfeld, 1854.

Subtribe **Eriopteraria**

Genus **Molophilus** Curtis (derivation obscure)

1833 *Molophilus* Curt. Brit. Ent., p. 444.

Larva.— Form long and slender. Spiracular disk squarely truncated and surrounded by five subequal lobes; paired lobes of disk heavily lined with black; a black mark running proximad from spiracles; dorsal lobe with an oval black area. Head capsule long and narrow; ventral rods flattened; anterior ends expanded, four-toothed, to form mental plates. Labrum narrow, densely hairy. Mandible blunt at apex; ventral cutting edge with about four teeth; a single subapical dorsal tooth. Maxilla large and blunt. Antenna large; apical papilla elongate-oval, sculptured.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns long and slender, sinuously curved. Mesonotum declivitous, at crest with four powerful teeth. Wing sheaths ending at about midlength of second abdominal segment. Leg sheaths ending at about midlength of fourth abdominal segment; tarsi of middle legs the shortest. Abdomen with spiracles on segments 2 to 7; dorsum of segment 8 with four blunt lobes.

Molophilus is a well-defined genus (including more than fifty species) of small and usually dull-colored flies, which are found practically thruout the world.

The adult flies frequent shaded situations and may be swept from rank vegetation in such places. The swarming habits of this group are discussed later under the specific accounts.

The immature stages of the various species are spent in wet earth. In Europe, *Molophilus obscurus* (Meig.) (Beling, 1879:56) and *M. ochraceus* (Meig.) (Beling, 1886:193–194) have been found in wet earth near running

water in shaded woods. The pupal duration of the latter species is not more than ten days. Keilin (1913 4) notes the presence of hypodermal glands in larvae of *M. bifilatus* Verr., but does not mention the larval habitat. Of the American species, *M. hirtipennis* has been reared from similar situations.

Molophilus hirtipennis (O. S.)

1859 *Erioptera hirtipennis* O. S. Proc. Acad. Nat. Sci. Phila., p. 228.

The little dark-colored crane-flies of the species *Molophilus hirtipennis* are common on vegetation in shaded woods in spring and early summer, or they may be found in small dancing swarms in similar situations.

The larvae are exceedingly abundant in wet organic mud or in cool, rich woods in the neighborhood of streams or springs. The writer has reared the species very frequently from specimens found in Needham's Glen and on Bool's hillside, Ithaca, New York, in April and May, 1914 to 1917. The pupal period is probably about a week, but in all the rearings of the writer this could not be ascertained closer than ten days.

Larva.— Length, 9–10 mm.
Diameter, 0.4–0.5 mm.

Coloration light yellow.

Form long and narrow; body terete, noticeably constricted before spiracular disk (Plate XLV, 344). Integument covered with a delicate appressed pubescence and a few transverse rows of very short, erect setae. Spiracular disk (Plate LXV, 351) squarely truncated, surrounded by five subequal lobes; ventral lobes on inner face with two heavy black parallel lines, separated by a capillary yellow line; lateral lobes with a similar double line running inward far beyond spiracle; these double lines not connected at distal end; dorsal lobe with a single oval black mark which is less intense outwardly; a black mark beginning at spiracle running proximad toward center of disk; lobes with a few short hairs at tips. (There is a little variation in the degree of intensity, but the general pattern is as described above.) Anal gills four, short and blunt.

Head capsule (Plate LXV, 345) long, narrow, consisting of six chitinized rods, the ventral rods broad and flat, at the anterior end expanded to form the mental plates (Plate LXV, 346), each rod contributing four teeth, of which the outermost is bluntly rounded, the middle pair the largest and subequal. Dorsal bars two on either side, one slender, at their anterior ends articulating with a transverse chitinized rod; the various bars connected by a thin membranous tissue. Labrum and epipharynx elongate, narrow, occupying the space between mandible and antenna on either side, the ventral face with abundant long hairs, on sides margined with numerous long, incurved, flattened setae. Mental plates as described above; behind them the hypopharynx (Plate LXV, 347), consisting of a semicircular cushion provided with dense, short setae. Antennae (Plate LXV, 348) rather closely approximated on dorsum, prominent, each 1-segmented but bearing a long apical papilla; basal segment moderately elongated, cylindrical, the apex obliquely truncated, the papilla hyaline, gradually narrowed

toward tip, shaped somewhat like an ear of corn, the surface delicately sculptured; besides this papilla, two or three much smaller cylindrical ones. Mandible (Plate LXV, 349) slender, ending in a blunt rounded lobe; ventral cutting edge with four blunt teeth, the second from the base very tiny and connected with the third from the base (in some specimens the teeth are very blunt and rounded, so that the cutting edge appears crenulated or wavy); a single tooth on dorsal cutting edge, immediately behind apex; prosthecal region of mandible with a longitudinal slitlike opening filled with a dense row of long setae. Maxilla (Plate LXV, 350) large and blunt, the outer lobe pale, roughly triangular, covered with numerous short hairs, and with a few small sensory papillae near apex, surrounding palpus; inner lobe a little shorter, densely clothed and fringed with abundant long yellow hairs.

Pupa.— Length, 6.2–7.3 mm.
Width, d.-s., 0.7–0.8 mm.
Depth, d.-v., 0.8–1 mm.

Head, thorax, and appendages brown, when fully matured almost black; breathing horns yellowish; abdomen pale yellowish white.

Cephalic crest of moderate size, consisting of two conical lobes directed forward and bearing a stout seta on anterior face; immediately in front of these, a smaller transverse crest lying between antennal bases. Front rather broad. Labrum triangular; lobes of labium triangular, divergent; maxillary palpi elongate, moderately stout, narrowed at tips and extending beyond joints of fore legs. Thorax prominent, carinate medially before declivity. Breathing horns long and slender, sinuously curved, apices directed forward. Declivity of mesonotum (Plate LXVI, 352) precipitous, at the crest armed with four powerful teeth, median pair the largest, somewhat divergent, separated by median line; a few tiny setae on mesonotum, including four in a transverse row at about the level of wing root. Wing sheaths ending opposite apex of second abdominal segment. (In fully matured pupae the characteristic venation of this genus shows on the wing pads.) Leg sheaths rather short, ending about opposite mid-length of fourth abdominal segment; hind legs slightly the longest, fore legs a little shorter, middle legs conspicuously shorter, ending about opposite apex of fourth tarsal segment of fore legs.

Abdominal segments with two very narrow basal rings and a much broader posterior ring. Abdominal spiracles distinct on segments 2 to 7. Setae as follows: on pleura, one immediately caudad of spiracle, a second caudad and somewhat dorsad of spiracle opposite posterior ring, another opposite anterior ring. Tergum with two setae on sides of posterior ring. Segment 8 with four blunt lobes on dorsum. Male cauda (Plate LXVI, 353 and 354) with ventral lobe large, bluntly rounded at tips; dorsal lobes ending in two acute, chitinized points which are widely separated and directed dorsad and slightly caudad, on outer face with a small seta; near base of cauda on dorsum, surface tumid and bearing a small seta on either side. Female cauda (Plate LXVI, 355 and 356) with sternal acidothecae much shorter than the very long tergal valves, these latter, just before apex, with an acute spine which is directed dorsad and with a seta on side. (When the pupa is nearly ready to transform to the adult, the long, coarse bristles covering the body of the adult, and the chitinized genitalia, show thru the pupal integument.)

Nepionotype.— Ithaca, New York, May 11, 1917. No. 33–1917.
Neanotype.— Ithaca, June 1, 1917.
Paratypes.— About one hundred larvae and pupae from type locality.

Molophilus ursinus (O. S.)

1859 *Erioptera ursina* O. S. Proc. Acad. Nat. Sci. Phila., p. 228.

Molophilus ursinus is probably the smallest crane-fly in North America. The following notes on the swarming were made along Power House Creek, Gloversville, New York, on June 27, 1915:

This species occurred in small dancing swarms over the little lateral streamlets that poured down the steep slope, some of the swarms including scores of individuals. When not swarming, they rested flat on the upper surfaces of leaves, their wings folded over the abdomen. Crane-flies associated with this species today included the following: *Bittacomorphella jonesi, Limnophila toxoneura, L. areolata, L.* (*Lasiomastix*) *tenuicornis, Liogma nodicornis, Dolichopeza americana, Tipula collaris, T. nobilis, T. iroquois, T. hermannia, T. macrolabis, T. submaculata, T. fuliginosa, Nephrotoma macrocera, N. tenuis, Longurio testaceus*, and others.

Genus **Erioptera** Meigen (Gr. *wool + wing*)

1800 *Polymeda* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Erioptera* Meig. Illiger's Mag., vol. 2, p. 262.
1818 *Polyraphia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 88.
1854 *Octavia* Bigot. Ann. Soc. Ent. France, p. 474.
1856 *Chemalida* Rond. Dipt. Ital. Prodr., vol. 1, p. 180.
1856 *Limnaea* Rond. Dipt. Ital. Prodr., vol. 1, p. 181.
1856 *Ilisia* Rond. Dipt. Ital. Prodr., vol. 1, p. 182.
1861 *Limnoica* Rond. Dipt. Ital. Prodr., Corrigenda, vol. 4, p. 11.
1863 *Trichosticha* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.
1864 *Platytoma* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 10, p. 42.

Larva.— Form elongate, in some cases very slender, terete. Spiracular disk tending to be reduced, in some species (as *E. chlorophylla*) very small. Anal gills blunt. Head capsule slender, consisting of six bars, four dorsal and two ventral; ventral bars in some species (as *E. chlorophylla*), at least, with five to eight teeth at their expanded anterior end, forming the mental plates. Labrum narrow, densely hairy. Mandible small, bluntly toothed. Maxilla blunt, hairy. Hypopharynx cushion-like.

Pupa.— Cephalic crest consisting of blunt or acute (in *E. chlorophylla* and *E. vespertina*) lobes. Pronotal breathing horns elongate, the length many times the diameter, usually straight and slightly divergent (*E. megophthalma, E. septemtrionis*), or acutely pointed and directed forward (*E. chlorophylla*). Mesonotal declivity along crest with very numerous setiferous tubercles or (in the European *E. lutea*) with four prominent teeth. Leg sheaths moderately long, reaching fourth abdominal segment; middle tarsi conspicuously shorter than the others. Subapical armature of abdominal segments strong on sternites and tergites but lacking on pleurites. Spiracles distinct, tubular. Lobes on dorsum of eighth abdominal segment not forming a distinct pentagon.

Erioptera is a large genus of small flies, including more than one hundred described species, chiefly from the temperate regions. In the case of all species of which the immature stages are known, these stages are spent in wet earth. In Europe, *Erioptera* (*Acyphona*) *maculata* (Beling, 1879,

49) was found under leaves in damp earth in woods. Pupae taken on June 8, 1874, emerged as adults on the 13th. The species was found also in the sandy mud of a small brook bed. *E.* (*E.*) *flavescens* (Beling, 1879: 50) was found in sandy, damp earth, *E.* (*E.*) *sordida* (Beling, 1879: 56, mention only) in wet, sandy earth along brooks, and *E.* (*E.*) *lutea* (Beling, 1886: 192–193) in woods, in damp hollows, and along the margins of brooks, usually under leaf mold. Edwards (1919 a) has recorded a species of Erioptera as being associated with the larvae of the mosquito Taeniorhynchus at the roots of water grass (*Glyceria fluitans*) in England.

In America, *E. chlorophylla*, *E. vespertina*, *E. caloptera*, and other species inhabit wet mud in open swamps; *E. septemtrionis* and *E. megophthalma*, rich organic mud in cool, shady woods; *E. armata*, *E.* near *knabi*, and other species, the soil along the sandy banks of streams. *E.* (*Acyphona*) *graphica* was considered by Hart (1898 [1895]: 197) to be semiaquatic.

The writer has before him the larvae of only two species of the genus, *E. chlorophylla* and *E. megophthalma*. These are readily separated by their color, *E. chlorophylla* being pale green, *E. megophthalma* pale yellow and more elongate. The pupae of the Nearctic species of the genus may be separated by the following key:

1. Breathing horns and cephalic crest strongly pointed and curved forward at their tips; coloration light green . . . . *E. chlorophylla* O. S. (p. 918)
   Breathing horns and cephalic crest not as above; coloration not green 2
2. Breathing horns elongate-cylindrical to slightly flattened, almost straight but slightly divergent, diameter subequal for entire length 3
   Breathing horns not as above, more or less curved, or else blunt at their tips 4
3. Cephalic crest sharply pointed; eyes large . . . . *E. megophthalma* Alex. (p. 915)
   Cephalic crest not sharply pointed; eyes small . . . . *E. septemtrionis* O. S. (p. 920)
4. Breathing horns almost straight, enlarged distally, tips blunt. *E.* sp. (near *knabi* Alex.) (p. 922)
   Breathing horns curved, narrowed toward tips 5
5. Breathing horns widely separated at base, bent strongly proximad, contiguous medially; lobes of cephalic crest acute, vertical; eyes large . . . . *E. vespertina* O. S. (p. 919)
   Breathing horns curved gently forward; cephalic crest with lobes directed laterad, divergent; eyes of moderate size . . . . *E. armata* O. S. (p. 921)

Erioptera megophthalma Alex.

1918 *Erioptera megophthalma* Alex. Can. Ent., vol. 50, p. 60–61.

The adult flies of *Erioptera megophthalma* are not uncommon in cool, shaded, and boggy woods during the months of early spring.

They may be swept from rich vegetation in company with such characteristic species as *Limnophila brevifurca*, *L. fuscovaria*, *L. subtenuicornis*, *Adelphomyia minuta*, *Rhaphidolabina flaveola*, *Molophilus hirtipennis*, *Erioptera venusta*, *E. stigmatica*, *Gonomyia florens*, *G. subcinerea*, and *Tipula oropezoides*.

The elongate larvae of this fly were very common in rich organic mud taken from Bool's hillside, Ithaca, New York (as discussed under the account of *Bittacomorphella jonesi*, page 780), where they were associated with a crane-fly fauna characteristic of such situations. The larvae, in life, are pale yellowish, with the food contents, of a chalky white color, showing thru the integument. The head capsule and the spiracular disk are very small; the inner face of each lobe of the latter is very narrowly lined with black. The species was reared many times during late May and early June, 1917, the length of the pupal existence indoors being seven or eight days.

Larva.— Length, 10.4–11.6 mm.
Diameter, 0.7–0.75 mm.

Coloration very pale yellow; contents of alimentary canal chalky white.

Form terete, elongated, body tapering gradually to the posterior end, just beyond gills (Plate LXVII, 358) suddenly constricted; last segment elongate-cylindrical, tapering gradually to the very small spiracular disk. Body covered with a short, appressed pubescence, on last segment this pubescence coarser and more erect, with a few elongate hairs interspersed; lateral parts of body at caudal margins of segments with short transverse lines of small, erect setae; a few other similar rows at about midlength of certain of the segments. Spiracular disk (Plate LXVII, 357) very small, tending to be eliminated by reduction; lobes short and blunt, dorso-median lobe the smallest; ventral lobes with two short brown lines, not connected distally, the proximal line a little longer than the lateral line of each lobe; the pale space between these lines a little less than diameter of one; lateral lobes with two similar divergent lines, the dorsal one attaining inner level of spiracles; dorsal lobe with two small, indistinct, brown lines; on disk between spiracles two small round spots which do not touch spiracles; lobes fringed with short hairs near tip, and capable of close approximation so that disk is often entirely closed. Spiracles large, nearly circular.

Head capsule small, very long and slender, greatly dissected, the three bars of either side long and delicate; dorsal bars at their articulation joined with a short longitudinal bar near whose anterior end the antennae are inserted; ventral bars of capsule not conspicuously expanded at their anterior end, and apparently not toothed as in other species of this genus and in Molophilus. Labrum and epipharynx long and narrow, lying between antennal bases; epipharyngeal region densely clothed with short setae at tip and with two parallel brushes on ventral face. Mentum apparently not formed as in *E. chlorophylla*, a slightly

arched transverse chitinized bar. Hypopharynx about as in Molophilus. Antennae rather closely approximated, directed cephalad; basal segment moderately elongated, cylindrical; apical papilla relatively small, elongate-oval. Mandible very small, with blunt teeth; apical point short, blunt; ventral row of teeth about three in number, often very blunt. Maxilla as in Molophilus, but outer lobe with the vestiture of hairs rather longer.

Pupa.— Length, 7.2–8.2 mm.
Width, d.-s., 0.8–0.9 mm.
Depth, d.-v., 1–1.1 mm.

Head light brown; thorax anterior to declivity conspicuously darker brown; remainder of body light yellowish brown; breathing horns light yellow. (In fully colored individuals the head and the thorax with their appendages become much darker, almost black, but the breathing horns retain their conspicuous yellow color.)

Head short, face tumid. Eyes of male very large, widely separated by front; eyes of female smaller. Cephalic crest consisting of two prominent lobes; viewed from side, these lobes sharply pointed and directed slightly forward, with a seta on outer ventral face before tips; viewed from front, lobes rounded, ending in acute tips, separated by a deep, rather narrow, V-shaped notch. Front between eyes narrowed toward labrum, which is rather sharply pointed. Labial sheaths small, the lobes contiguous with their apices truncated, the lateral angles obtuse or produced into a tiny lobe. Sheaths of maxillary palpi short and stout, tapering gradually to tips. Antennal sheaths moderately elongated, angulated at segments, ending just beyond base of wing. Pronotal breathing horns stout, expanded at base, almost straight and only slightly divergent, somewhat compressed, transversely wrinkled basally; a small setiferous tubercle in front of base of breathing horn. Mesonotum precipitous, at crest (Plate LXVII, 359) on either side of median line with abundant tiny setiferous tubercles bearing long, pale hairs, these tubercles continued back along shoulder. Lateral margin of thorax with two small setae. Wing sheaths ending before tip of second abdominal segment. Leg sheaths (Plate LXVII, 360) short, attaining base of fourth abdominal segment; tarsi of hind legs the longest, those of middle pair the shortest; fore legs with femora and tibiae very short.

Abdominal segments (Plate LXVII, 361) divided into two annuli by a constriction near midlength, the anterior ring very indistinctly subdivided further into two lesser annulets; on segments 4 to 7, before caudal margin of posterior ring on both dorsum and sternum, a transverse row of small, conspicuous, blackened, setiferous tubercles, which are more distant from one another near ends of rows; on basal abdominal segments these tubercles less evident but still present. Pleura with small but probably non-functional spiracles, which are very indistinct in young pupae but are more evident in fully colored individuals; these spiracles located near base of posterior ring. Setae on abdomen as follows: on sternal segments, one seta just caudad of end of row of spicules, a second at lateral end of this row, intermixed with spicules, two on posterior ring on a level with spicules; on tergal segments, a strong seta on a line with spiracles, another seta below end of row of spicules; on pleura, one seta just ventrad of spiracles, and two post-spiracular and one ante-spiracular setae. Male cauda (Plate LXVII, 362 and 363) with ventral lobes obliquely truncated, blunt at tips, projecting beyond level of subacute dorsal lobes; dorsal lobes slender, slightly divergent apically, blackened before tips and with two setae at tips on outer face; at base of cauda,

on dorsal face of eighth segment, a close quadrangle of four rounded tubercles, placed on a slight elevation. Female cauda with tergal acidothecae elongate, subacute at tips; sternal valves short, blunt; quadrangle of tubercles on dorsum of eighth segment more distinct than in the male.

Nepionotype.— Ithaca, New York, May 14, 1917.
Neanotype.— Ithaca, June 5, 1917.
Paratypes.— Larvae and pupae in large numbers from type locality, May 14 to June 5, 1917.

Erioptera chlorophylla O. S.

1859 *Erioptera chlorophylla* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera chlorophylla is conspicuous by its pale green color in the larval, pupal, and adult stages. It is a common and widely distributed species thruout eastern North America. Several larvae were found in organic mud at Orono, Maine, on June 13, 1913, one of which pupated on the 21st. When the insect is dropped into boiling water, the green color immediately disappears. The associates of this species are discussed under the account of *Ptychoptera rufocincta* (page 775).

Larva.— Length, 9–10 mm.
Diameter, 0.7–0.75 mm.

Color uniformly pale green, fading to a pale yellow after death.

Form moderately elongated, last segment of body elongate, gradually narrowed to bluntly rounded apex. Body clothed with numerous appressed hairs. Spiracular disk somewhat as in *E. megophthalma* but even more reduced, disk usually entirely closed, lateral lobes on either side capable of close approximation, tracheae before the opening into spiracles very large.

Head capsule (Plate LXVIII, 364) of the Molophilus type, but longer and slenderer; the two dorsal bars of each side very delicate, the ventral bars broader and flattened. Mental plates (Plate LXVIII, 365 and 366) slender; anterior end of each ventral bar widely expanded and provided with several teeth; these teeth varying in number, in some specimens there being only five, in others eight, teeth to each plate; in the latter case the third from either side is larger, with two smaller teeth between. Hypopharynx about as in Molophilus. Antenna (Plate LXVIII, 367) large, basal segment stout, cylindrical; apical papilla elongate-oval, with apex bluntly rounded and surface weakly sculptured; laterad of this papilla a tiny cylindrical hyaline peg. Mandible (Plate LXVIII, 368) rather large; cutting edge with about four slender teeth, the second from base the smallest; dorsal face of mandible with a blunt subapical tooth and an oblique comb of about six stout setae or chitinized teeth. Maxilla similar to that of Molophilus, but the hairy vestiture longer and coarser.

Pupa.— Length, 8.8–9 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.2 mm.

Breathing horns reddish brown; thoracic dorsum green, with a brownish tinge; abdomen uniformly pale green, posterior half of each dorsal segment a little darker.

Cephalic crest small and compact, consisting of two prominent but closely approximated lobes which are separated by a deep U-shaped notch, the tips acute and directed forward; on outer face before apex a short seta. Labrum broadly obtuse at tip. Labial lobes roughly triangular, divergent. Maxillary palpi short and stout, narrowed toward tip. Antennal sheaths with a slender tubercle at base above eye.

Pronotal breathing horns broad at base, narrowed to the acute tip which is directed almost ventrad; viewed from above, horns very broad basally and with a dorsal carina; ventral side at base transversely wrinkled; a small setiferous lobe just in front of breathing horns, directed laterad. Mesonotum behind breathing horns with a high compressed carina, on either side of this produced into a lobe directed cephalad and laterad; mesonotum moderately declivitous (Plate LXIX, 369), at crest with numerous setiferous tubercles which are fewer in number and more widely separated along shoulder. Leg sheaths reaching to about middle of fourth abdominal segment; hind legs a little longer than fore legs; middle legs very short, ending opposite base of last segment of fore legs.

Abdominal segments divided into two narrow basal rings and a broad posterior ring; on pleura a distinct spiracle, opposite posterior annulus and nearer dorsal margin; posterior annulus, before caudal margin, with a dorsal and a ventral row of long, stout setae. Setae on abdomen as follows: on pleura, a seta opposite second basal ring, a second ventrad of spiracle, and two setae caudad of spiracle, the posterior one a little more dorsal in position; on tergites, two stout setae lying transversely on the margin opposite spiracle, a third seta at end of terminal rows of bristles; on sternites, a group of two transverse setae on posterior ring, slightly below level of spiracle and rather widely separated by the broad midventral area. Female cauda (Plate LXIX, 370) with dorsal acidothecae short, distinctly upturned, and ending in a small, subacute tip; before apex with two very short setae; a short blunt tubercle near base of valves; ventral lobes short, their tips very blunt; dorsum of segment 8 with two blunt median tubercles, one immediately behind the other.

(Described from larvae taken in the Basin Swamp, Orono, Maine, June 13, 1913; one pupa with the larva, July 5, 1913.)

Erioptera vespertina O. S.

1859 *Erioptera vespertina* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera vespertina is a characteristic inhabitant of open swamps and wet meadows. It has not been reared, but a pupa found in organic mud in the Basin Swamp, Orono, Maine, on June 24, 1913, undoubtedly belongs to this species. The associates are discussed under the account of *Bittacomorpha clavipes* (page 785).

Pupa.— Length, 8.5 mm.
Depth, d.-v., 1.1 mm.

Breathing horns reddish brown; thoracic dorsum reddish brown, with an interrupted whitish line running down posterior half of mesonotum; sheaths of wings and legs pale

brown; abdomen whitish yellow, posterior half of each sternite and tergite dark brown, basal half with two narrow transverse lines of same color.

Lobes of cephalic crest widely separated, subtriangular, acutely pointed at tips. Pronotal breathing horns cylindrical, transversely wrinkled, tapering gradually to tips. (In the only specimen at hand, the horns are widely separated at the base but soon bend proximad and thence outward and ventrad, so that the two horns are closely approximated or almost contiguous on their distal parts.) Behind breathing horns, mesonotum with conspicuous divergent lobes such as are described for *E. chlorophylla*; mesonotum at crest with abundant black setiferous tubercles, which are fewer in number, smaller, and more scattered along shoulder, interrupted at mid-dorsal line. Hind legs a little longer than fore legs, which, in turn, are a little longer than middle legs.

Abdominal segments with subterminal armature of posterior ring more spinous than in *E. chlorophylla*. Distribution of setae about as in *E. chlorophylla*.

(Described from a pupa taken at Orono, Maine, June 24, 1913.)

Erioptera septemtrionis O. S.

1859 *Erioptera septemtrionis* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Erioptera septemtrionis is a widely distributed species thruout the northeastern United States and Canada. The larvae are not uncommon in rich organic mud in cool, shaded woods. The writer found them commonly in the Standpipe Woods, Orono, Maine, in July and August, 1913. A larva placed in rearing on July 3 transformed to an adult female on the 16th. Other larvae placed in rearing on July 15 transformed to adult males on the 25th. This limits the pupal duration to not more than ten days, but it is probably much less, presumably about one week.

Pupa.— Length of cast skin, 7 mm.

Cephalic crest low and flat. Antennal sheaths moderately elongated, individual segments showing clearly thru sheaths. Pronotal breathing horns elongate, cylindrical, almost straight but slightly diverging, transversely wrinkled, paler at tips, with a row of small breathing pores along apical margin; a few small setiferous tubercles before base of breathing horns. Declivity of mesonotum rather steep, at crest with numerous small tubercles and abundant pale yellow hairs which are less numerous along shoulder. Leg sheaths with middle pair conspicuously the shortest, as in the genus.

Abdominal segments with subterminal armature of posterior ring consisting of stout, pale setae; arrangement of these setae about as in *E. chlorophylla*. Lateral spiracles distinct. Male cauda (Plate LXIX, 371 and 372) with the ventral lobes blunt at tips, obliquely truncated, separated by an acute V-shaped notch; dorsal lobes separated by a U-shaped notch, each lobe terminating in a small tip, with two tiny setae on lateral face before apex; dorsum of eighth segment with four prominent, pale, fleshy lobes which are closely approximated, the anterior pair directed laterad and a little more distant from each other than the posterior pair, which are directed more dorsad.

Neanotype.— Orono, Maine, July 25, 1913. No. 105-1913.

(Subgenus **Hoplolabis** Osten Sacken)

1869 *Hoplolabis* O. S. Mon. Dipt. N. Amer., part 4, p. 160.

The subgenus Hoplolabis includes but three known species — the type of the group, *Erioptera* (*Hoplolabis*) *armata*, discussed below; *E.* (*H.*) *bipartita* O. S., of western North America; and *E.* (*H.*) *asiatica* Alex., of Japan.

Erioptera (*Hoplolabis*) *armata* O. S.

1859 *Erioptera armata* O. S. Proc. Acad. Nat. Sci. Phila., p. 227.

Erioptera armata is a rather common fly thruout the northeastern United States. A larva was found in the sand along the banks of Fall Creek, Ithaca, New York, on May 16, 1917. This larva was of the typical eriopterine form, being elongate, terete, and with the spiracular disk surrounded by five subequal lobes. It was placed in rearing and transformed to an adult female on May 31. This larva was found associated with numerous hexatomine larvae, such as *Eriocera spinosa*, *E. longicornis*, and *E. cinerea*.

The following description is from the cast pupal skin.

Length, about 7 mm.

Cephalic crest consisting of two moderately large, slightly divergent lobes which are acutely pointed at tips; lobes directed strongly outward and bearing a seta on outer face. Labrum acutely pointed. Labial lobes large, divergent, almost straight across caudal margin. Sheaths of maxillary palpi stout, rather pointed at tips. Pronotal breathing horns broad at base, tapering to slender apices, bases conspicuously wrinkled; a small setiferous tubercle before base of each breathing horn. Mesonotum at crest (Plate LXIX, 373) with numerous short, chitinized points. Lateral angle of thorax with two setae; a strong seta above wing axil. Leg sheaths with middle tarsi ending conspicuously before tarsi of other legs.

Each abdominal segment before posterior margin with a transverse row of slender black spicules or short bristles on tergum and sternum, and smaller areas on pleura. Lateral abdominal spiracles distinct. Setae on pleura just ventrad of spiracle, and on tergum just above transverse row of spicules. Female cauda with tergal valves elongated, gently upcurved, unarmed; sternal valves shorter, blunt; at base of cauda, on dorsum of eighth segment, four small darkened tubercles which are produced into slender tips.

Neanotype.— Cast pupal skin, Ithaca, New York, May 31, 1917.

(Subgenus **Mesocyphona** Osten Sacken)

1869 *Mesocyphona* O. S. Mon. Dipt. N. Amer., part 4, p. 161.

Mesocyphona is one of the larger subgenera of Erioptera, reaching its maximum of specific development in the Tropics of the New World.

The immature stages of *Erioptera* (*Mesocyphona*) *caloptera* (Say) and *E.* (*M.*) *parva* O. S. are spent in wet mud along the banks of streams and other bodies of water. The species discussed below as *Erioptera* (*Mesocyphona*) species (near *knabi*), was reared from the sandy margins of a small prairie stream in Kansas.

Erioptera (*Mesocyphona*) species (near *knabi* Alex.)

Adult flies of a small species of Mesocyphona which is close to *E.* (*M.*) *knabi* Alex., of Mexico, were not uncommon along Buckner Creek, a small prairie stream flowing thru Jetmore, Kansas. These adults, especially the females, were photophilous, appearing in considerable numbers around lanterns which were hung in tents pitched along the banks of this stream. A single pupa found in the muddy sand along the bank of the creek on July 20, 1917, emerged as an adult on the 22d. The following general characters of the species may be noted:

Pupa.— Labrum small, apex rather sharp. Labial lobes squarely truncated, with lateral angles subacute. Sheaths of maxillary palpi slender. Pronotal breathing horns moderately long, cylindrical, curved slightly forward, enlarged outwardly, blunt at tips. Mesonotum at crest rather tumid and with a few long hairs inserted on stout black tubercles. Leg sheaths with middle tarsi the shortest, hind tarsi the longest.

Neanotype.— Jetmore, Hodgeman County, Kansas, July 22, 1917.

Genus **Ormosia** Rondani (Gr. *chain*)

1856 *Ormosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 180.
1860 *Rhypholophus* Kol. Wien. Ent. Monatschr., vol. 4, p. 393.
1863 *Dasyptera* Schin. Wien. Ent. Monatschr., vol. 7, p. 221.

Larva.— Form terete, moderately elongated. Spiracular disk squarely truncated, surrounded by five subequal lobes which are lined with double marks of brown. Anal gills blunt. Head capsule slender, very dissected, of six narrow bars, four dorsal and two ventral, the ventral bars broader. Labrum narrow, epipharynx hairy. Mandible with teeth moderately elongated. Antenna of the Molophilus type. Mentum without chitinized teeth.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns rather short and stout, more or less flattened and with a row of tubercles along posterior margin. Mesonotum declivitous, at crest with a flattened, toothed, chitinized plate on either side (in *O. nubila*) or with abundant setiferous tubercles. Wing sheaths ending opposite or just beyond tip of second abdominal segment. Leg sheaths varying in length with the different species, middle tarsi the shortest. Abdominal segments with a subterminal transverse row of spines or setae, these occurring on pleura (as small groups of eight to twelve) as well as on tergites and sternites. Lateral spiracles distinct, on segments 2 to 7; dorsum of segment 8 with

a pentagon of five lobes, these being unarmed (*O. innocens, O. meigenii*) or spinous-tipped (*O. nubila, O. nigripila*).

Ormosia is a large and rather difficult genus (including more than seventy-five species) of small crane-flies which are characteristic of sub-arctic and temperate regions and apparently rare or lacking in the Tropics.

The adult flies occur in small dancing swarms, usually in cool, shaded situations in or near woods or along brooks. They are most numerous in early spring and in late summer or early autumn, many of the species being apparently double-brooded.

The immature stages are spent in moist organic mud near water. In Europe, Beling records *Ormosia haemorrhoidalis* (Zett.) (Beling, 1879: 48–49, and 1886:191–192), *O. lineata* (Meig.) (Beling, 1886:202), and *O. nodulosa* (Macq.) (Beling, 1886:202), as being found in wet earth in woods, usually beneath leaf mold. Cameron (1917:65) likewise records the last-named species as living in mud. *O. varia* (Meig.) was found by De Meijere (1916:201–204) among decaying leaves in a wet spot near a ditch.

Of the American species, the writer has bred *Ormosia innocens, O. nubila, O. meigenii*, and *O. nigripila* from larvae or pupae in entirely similar situations to those given above for the European species.

The larvae of only two of these species, *O. nubila* and *O. meigenii*, are available to the writer at this time. *O. nubila* is a large brown species; *O. meigenii* is much slenderer, and is light yellow in color.

The pupae of the known Nearctic species may be distinguished as follows:

1. Dorsum of eighth abdominal segment with a pentagon of five lobes which are spinous at their tips 2
   Dorsum of eighth abdominal segment with a pentagon of five fleshy lobes 3
2. Crest of mesonotum with a flattened chitinized plate on either side of median line. *O. nubila* (O. S.) (p. 923)
   Crest of mesonotum tumid, with abundant coarse, yellowish setae on either side of median line . . . . . . *O. nigripila* (O. S.) (p. 927)
3. Abdomen with large, rectangular, dusky areas on posterior annuli of segments 2 to 8, giving abdomen a banded appearance; pleural setae rather numerous. *O. innocens* (O. S.) (p. 925)
   Abdomen without such dusky areas; pleural setae few in number. *O. meigenii* (O. S.) (p. 928)

Ormosia nubila (O. S.)

1859 *Erioptera nubila* O. S. Proc. Acad. Nat. Sci. Phila., p. 227.

Ormosia nubila is probably double-brooded, since the flies are on the wing in the spring and again in the fall. The immature stages live in

organic mud that is usually covered over with a layer of leaf mold. On March 27, 1914, the writer found four large brown eriopterine larvae in rich earth from Needham's Glen, Ithaca, New York. An adult female of the present species emerged on April 9. This makes the maximum pupal existence less than two weeks, but it is undoubtedly very much less than this.

Larva.— Length, 11.5–11.8 mm.
Diameter, 1.1–1.2 mm.

Color a deep reddish or cinnamon brown; incisures of segments paler.

Form rather stout, body terete. Skin covered with a short, appressed pubescence. Spiracular disk (Plate LXX, 375) squarely truncated, surrounded by five subequal lobes; ventral lobes with two parallel dark brown lines which are narrowly united distally, the pale stripe between rather broad, distinct, especially near center of disk; lateral lobes with two parallel dark brown stripes which are indistinctly connected distally, the space between dusky with numerous brown spots; dorsal lobe with an elongate-oval mark inclosing a linear yellow center; lobes fringed with long hairs which are longest at tips, shorter toward base, and narrowly interrupted between lobes; disk between spiracles unmarked. Spiracles large; middle piece and extreme outer margins of ring blackish; spiracles separated by a distance about equal to one and one-half times diameter of one.

Head capsule about as in Molophilus, but ventral bars of capsule not toothed to form the characteristic mental plate of that genus. Labrum and epipharynx about as in Molophilus. Hypopharynx broad, flattened, provided with numerous transverse rows of short setae. Antenna short; basal segment stout, cylindrical; apical papilla rather small, elongate-oval. Mandible (Plate LXX, 374) ending in a rather long apical point, with about four long, flattened teeth along ventral cutting edge, the second from base very small; a short, recurved hook at prosthecal region and a dense tuft of long yellow hairs in prosthecal slit; a dorsal appendage at heel of mandible. Maxilla about as in Molophilus.

Pupa.— Length, 7.5 mm.
Width, d.-s., 1.2 mm.
Depth, d.-v., 1.4 mm.

Head, thorax, and appendages pale yellow; breathing horns yellow; chitinized plates on mesonotum dark brown; abdomen brown. (In mature pupae, the sheaths of the appendages are probably darker.)

Cephalic crest (Plate LXXI, 381) low; lateral angles produced into conical, erect, spinous tubercles, each bearing a stout seta on outer ventral face. Antennal sheaths very angulated, almost serrate. Opposite each segment of antenna on basal half of organ, a conspicuous blackened tubercle, those at base larger and more conspicuous, the lateral one directed outward, above it a second tubercle directed cephalad and simulating a crest. Antenna extending to just beyond base of wings. Front broad; a blackish area on either side near inner margin of eye, probably indicating point of attachment of tentorium. Labrum triangular, apex subacute. Labial lobes triangular, tips blunt. Sheaths of maxillary palpi rather long, narrowed to the slender tip. Pronotal breathing horns short and slender, some-

what flattened, pale yellow; a stout seta just before base of each breathing horn. Mesonotum precipitous; at crest (Plate LXXI, 380) on either side of median line, a heavily chitinized flattened plate projecting dorsad; this plate, at its tip, forking into two lesser teeth, the lateral one of these still further subdivided into two still smaller teeth (in one specimen the left plate is divided dichotomously into four teeth, the inner primary tooth being further subdivided); on shoulder laterad of these plates a slightly swollen plate which is parallelly grooved; two spines on lateral angle of thorax above base of wing; mesonotum with a few setae behind crest, as follows: an anterior solitary seta on either side of median line and close to it, a solitary stout seta above wing axil, two groups of paired setae, one just dorsad of base of wing and the other midway between this group and the anterior seta first described. Wing sheaths rather short, ending opposite base of third abdominal segment. Leg sheaths rather long for this genus, ending opposite midlength of fifth abdominal segment; fore tarsi a little shorter than hind tarsi, middle tarsi very short, ending opposite or just beyond end of third tarsal segment of fore legs.

Abdominal segments near posterior margin with transverse rows of short black spineg which are much smaller and more widely separated near ends of row; at intervals alona row a few elongate setae; on pleura a similar area of eight to eleven spines with a single sets in row; tubular lateral spiracles on segments 2 to 7. Chaetotaxy as follows: on pleura, just above dorsal end of row, one seta, another solitary seta cephalad of spiracle on anterior ring; on tergites, a solitary seta on posterior ring about opposite spiracle; on sternites, two small setae on either side of median line of posterior ring. Female cauda (Plate LXXI, 382) with tergal valves long and slender, almost straight but slightly upcurved near tips; on dorsal lateral margin, just before tip, a prominent tooth directed laterad and slightly caudad; about midlength of valves a somewhat similar blunt tubercle on either side near dorsal margin; at base of eighth tergite a pentagon of five chitinized lobes, the anterior one rudimentary, the four developed lobes ending in acute chitinized points and each bearing a subapical seta; anterior pair of lobes more widely separated and bearing on lower side near base a small, slender lobule.

Nepionotype.— Ithaca, New York, March 27, 1914.
Neanotype.— Ithaca, with type larva, April 9, 1914. No. 2–1914.
Paratypes.— With types.

Ormosia innocens (O. S.)

1869 *Rhypholophus innocens* O. S. Mon. Dipt. N. Amer., part 4, p. 142.

Ormosia innocens is a characteristic early spring species, the adult flies being found in late April and during May. On May 12, 1917, a few pupae in an advanced stage of development were sifted from organic mud from Bool's hillside, Ithaca, New York. One of these emerged as an adult on the following day. The associated crane-fly larvae that occurred with this species on the date named were as follows: *Bittacomorphella jonesi*, *Dicranomyia stulta*, *Limnophila adusta*, *L. fuscovaria*, *Ulomorpha pilosella*, *Penthoptera albitarsis*, *Rhaphidolabina flaveola*,

Molophilus hirtipennis, Erioptera megophthalma, Ormosia nigripila, Tipula oropezoides, T. collaris, T. cayuga.

Pupa.— Length, 7.5–10.5 mm.
Width, d.-s., 0.8–1 mm.
Depth, d.-v., 1–1.2 mm.

(The smaller measurements are those of males, the larger those of females.)

Head and thorax brown; mesonotum before declivity darker brown; abdomen pale yellowish white, the sternal and tergal sclerites with broad, rectangular, darker areas, producing a banded appearance; breathing horns pale yellow. (In older pupae, the coloration of the head and the thorax is much darker.)

Cephalic crest of moderate size, bilobed; viewed from side, lobes blunt, with two lateral setae; viewed from front, lobes separated by a very broad, V-shaped notch. Between antennal bases, forehead longitudinally grooved, these lines converging between eyes. Labrum triangular, subacute, separating the small labial lobes. Maxillary palpi of moderate length, tapering to blunt apices. Antenna of moderate length, reaching to just beyond wing base. Pronotal breathing horns rather short and stout, almost straight and only slightly diverging, subcylindrical, compressed, and slightly constricted just beyond base. Mesonotum precipitous, carinate medially; at crest (Plate LXX, 376) with numerous pale hairs, these narrowly interrupted on median line; lateral angle of thorax with two tiny setae; a strong seta slightly dorsad and cephalad of wing root; about four small setae in alinement across mesonotum. Wing sheaths moderately broad, ending at or just before tip of second abdominal segment. Leg sheaths short, tips of all the tarsi ending about on a level, or those of fore legs a little longer, terminating just before end of third abdominal segment.

Abdominal segments divided into two distinct annuli by a constriction at about mid-length of segment; sternum and tergum of posterior ring of segments 2 to 8 near caudal margin with large, rectangular, dusky areas which appear subchitinized; caudal margin of this area with a fringe of long, black hairs, there being about seventy-five of these on intermediate segments; on pleural membrane a very small, similar area bearing from twenty-five to thirty-nine hairs, and near its dorsal margin a distinct black tubular spiracle on segments 2 to 7; the following additional setae on segments: on dorsal segments, rectangular darkened areas with sparse scattered elongate hairs over surface, and two setae on each anterior ventral angle, their arrangement oblique; sternal segments similar, but the two setae on rectangular area arranged transversely; just caudad of ends of fringe of hairs, one or two isolated hairs; pleural membrane opposite basal annulus with a single seta; another seta opposite posterior annulus near ventral margin; a third seta on ventro-cephalic angle of pleural setiferous area just above level of spiracle; segment 8 on dorsum with five pale, gill-like lobes arranged in a quadrangle or a pentagon, the anterior lateral pair the longest, the median one rather the smallest; at base of anterior pair, two setae on cephalic face; at base of posterior pair, a single seta on lateral face. Male cauda (Plate LXX, 377 and 378) terminating in two very blunt ventral lobes and two separated, slender, dorsal lobes projecting caudad and dorsad. Female cauda similar to male cauda, but tergal acidothecae very elongate, much longer than sternal valves.

Neanotype.— Ithaca, New York, May 12, 1917.
Paratypes.— Seven pupae, with type.

Ormosia nigripila (O. S.)

1869 *Rhypholophus nigripilus* O. S. Mon. Dipt. N. Amer., part 4, p. 142.

The larvae of *Ormosia nigripila* are common in rich organic mud in shady places. Larvae found in Needham's Glen, Ithaca, New York, on March 27, 1914, emerged on April 18. Other larvae from Coy Glen, found on April 17, emerged on May 1. At Orono, Maine, large larvae were found on July 14, 1913, and were placed in rearing, emerging on the 26th as adult males. This limits the pupal duration to not more than two weeks, but it is undoubtedly much less, probably not more than a few days or a week.

Pupa.— Length, 5.2 mm.
Width, d.-s., 0.9 mm.
Depth, d.-v., 1 mm.

Head, thorax, and appendages light brown, becoming darker in maturity; breathing horns and abdomen pale whitish.

Cephalic crest with lobes small, low, and rounded, with a powerful seta at tip, directed forward. Labrum blunt at apex. Labial lobes large, subtriangular, lateral angles obtusely pointed. Sheaths of maxillary palpi stout, rather elongate. Pronotal breathing horns (Plate LXXII, 384) rather short and flat, compressed, slightly expanded beyond base; outer, or posterior, margin with about five small tubercles, at least one of which is setiferous. Mesonotum very steep and precipitous, as in this group of species; crest (Plate LXXII, 383) tumid, extensive, on either side with abundant coarse yellow bristles; caudad of these, four stout setae in a quadrangle, two on either side of median line; lateral angles of thorax with two stout setae; a strong seta just above wing base. Wing sheaths reaching base of third abdominal segment. Leg sheaths moderately long, extending almost to midlength of fourth abdominal segment; tarsi of middle legs much shorter than the others, hind legs a very little longer than fore legs.

Abdomen with segments (Plate LXXII, 385) before their caudal margin bearing transverse rows of slender spines; pleura with a small area lying a little cephalad of tergal and sternal rows and margined behind with eight to ten spines. Spiracles distinct, tubular. Setae as follows: on pleura, a seta on anterior annulus, a stout seta just ventrad of spiracles, and a third lying a little ventrad and cephalad of spiracle; on sternites, two stout setae near base of posterior annulus; on tergites, two setae on posterior annulus, lying transversely at level of spiracle, and a third seta just cephalad of end of row of spines. Male cauda (Plate LXXII, 386) with ventral lobes rather slender, narrowed outwardly, and somewhat pointed at apex; dorsal lobes curved strongly backward, terminating in acute, chitinized points with a strong seta on outer face before tip and a second seta nearer base; dorsum of segment 8 with five brown, chitinized lobes which are crowned at their apices with a circlet of spines; posterior pair the longest and stoutest, broad at base, more slender outwardly, with a large lateral spine and about three smaller inner spines; anterior pair more slender; median lobe slender, crowned with a circlet of about six small, subequal spines. Female cauda (Plate

LXXII, 387) with dorsal terebra elongate, almost straight or very slightly upturned; eighth segment with dorsal pentagon of spine-tipped lobes quite as in male.

Ormosia meigenii (O. S.)

1859 *Erioptera meigenii* O. S. Proc. Acad. Nat. Sci. Phila., p. 226.

Ormosia meigenii is one of the commonest species of the genus, occurring in small dancing swarms in early spring. Larvae of this species were taken on April 10, 1914, in organic mud from Needham's Glen, Ithaca, New York. An adult female emerged on May 4.

Larva.— Length, 6.5 mm.
Diameter, 0.5–0.6 mm.

Color, light yellow.

Form elongate, terete. Spiracular disk (Plate LXX, 379) about as in *O. nubila*, dorso-median lobe the smallest, ventral lobes with brown lines rather close together, the distal line the broadest; lateral lobes with lines rather short, not contiguous at their distal ends and not extending past midlength of spiracles; dorso-median lobe with marks oval, solidly dark brown. Lobes fringed with moderately long, yellowish setae, which are almost lacking at extreme tips; disk between spiracles unmarked. Spiracles large, transversely oval, separated by a distance a little greater than the long diameter of one.

Head capsule and mouth parts almost as in *O. nubila;* mandible with the long, slender teeth of that species.

Pupa.— (Described from a cast skin.)

Cephalic crest consisting of low, rounded lobes, each with a seta on anterior lateral face. Pronotal breathing horns of moderate length, flattened, a little narrowed toward tip, outer margin with fine tubercles. Mesonotum not so declivitous as usual in the genus, with tiny roughenings at crest; the usual two setae at lateral angle of thorax present, another above each wing, and four more in a transverse row at level of axilla of wing; a seta on mesonotum, close to median line, just below crest. Middle legs much shorter than fore and hind legs.

Subterminal rows of setae on abdominal segments consisting of slender, acute spines, with a few setae interspersed; on pleura the spines few in number. Spiracles elongate, tubular. Female cauda with tergal sheaths very long, sternal sheaths short, their tips blunt; on dorsum of eighth abdominal segment five small unarmed tubercles, which are blunt or nearly so, anterior pair more widely separated than posterior pair. (In the shape of the cephalic crest, the breathing horns, and the declivity of the mesonotum, this species resembles *O. nigripila*; but the arrangement of setae on the abdomen, and the great reduction and unarmed condition of the lobes on the eighth abdominal tergite, are distinctive.)

Nepionotype.— Ithaca, New York, April 10, 1914.
Neanotype.— Cast pupal skin, Ithaca, May 4, 1914.

Genus **Helobia** St. Farg. et Serv. (Gr. *marsh* + *I live*)

1825 *Helobia* St. Farg. et Serv. Encyclop. Method. Ins., vol. 10, p. 585.
1830 *Symplecta* Meig. Syst. Beschr., vol. 6, p. 282.
1865 *Idioneura* Phil. Verh. Zool.-Bot. Ges. Wien, vol. 15, p. 615.
1886 *Symplectomorpha* Mik. Wien. Ent. Zeitung, vol. 5, p. 318.

Larva.— Form moderately elongated, body terete. Spiracular disk surrounded by five subequal lobes which are marked with V-shaped brown lines, in some specimens the inner faces of the three most dorsal lobes being entirely brownish black. Anal gills moderately elongate. Head capsule as in the Eriopterini. Antenna with the apical papilla very short, subpyriform.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns elongate-cylindrical, directed ventrad and cephalad, with rows of breathing pores along dorsal face. Mesonotum declivitous, at broad crest armed with numerous chitinized spines; an arcuated longitudinal row of six small pits extending from wing axil toward crest of thorax. Wing sheaths ending before tip of second abdominal segment. Leg sheaths ending about opposite tip of third abdominal segment; tarsi of hind legs the longest, those of middle legs the shortest, fore legs intermediate in length. Abdominal segments with a strong subterminal armature on ventral segments, much weaker to lacking on dorsal segments; lateral spiracles distinct on segments 2 to 7; dorsum of segment 8 with five blunt lobes.

Helobia is a small genus (five species) of common and sometimes very widely distributed crane-flies. The only North American species, *Helobia hybrida*, is apparently the most widespread tipulid known, ranging over practically the entire Holarctic region, southward in the mountains to India, and, in the New World, to Central America. The immature stages of the known species are spent in moist earth near water. Bruch (*in litt.*) mentions the rearing of *H. macroptera* (Phil.) in Argentina.

Helobia hybrida (Meig.)

1804 *Limonia hybrida* Meig. Klass., vol. 1, p. 57.
1818 *Limnobia punctipennis* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 147.
1830 *Symplecta punctipennis* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, p. 283.
1848 *Limnobia cana* Walk. List Dipt. Brit. Mus., vol. 1, p. 48.

Helobia hybrida is undoubtedly the most widely distributed North American crane-fly. Beling (1879:50–51) found larvae and pupae at the end of July, 1876, in wet, sandy earth along the margins of small brooks in deciduous woods. Adults emerged in his breeding cages on July 27 and August 6. Hart (1898 [1895]:199–200) found the larvae in similar sandy situations along the Illinois River, associated with the larvae of *Tabanus atratus* Fabr. He suggests that it may serve as food for this horse-fly larva. Larvae of Helobia were especially abundant on May 17, and these transformed to adults within a month. Females were observed ovipositing along the shore, patting the valves of the ovipositor against the moist sand. Malloch (1915–17b:229–230) has given additional notes on the structural details of Hart's material.

Dr. Adam Böving found this species in Iceland and made careful notes on the burrows made by the larvae. Thru the kindness of Dr. Böving, the writer is able to include a translation of his manuscript. The writer is indebted also to Dr. Lundbeck, director of the museum at Copenhagen, for the loan of this material for study. These are the specimens discussed later in this paper. Böving's notes were made at Fell Station, southeast Iceland, in 1908. The translation follows:

Inside the moraine of 1877, in the low land where ice was standing in 1886, quantities of dipterous larvae were found in the moist sand on the bottom of flat hollows which at times are flooded by water and at times are partly drained, as was the case on the day when the following observations were taken.

The whole dark, moist surface of the bottom was covered by an irregular system of slightly elevated, long, tubular galleries, some of which were rather straight, some formed broken lines, some peculiar arabesques, and some plain spirals. The width of the galleries was about the size of an ordinary pinhead, some a trifle larger, some a little smaller. In the anterior part of each gallery was found either a cylindrical white tipulid larva (Helobia) about one centimeter long, or another dipterous larva of the same general size and appearance. The larvae were found just below the surface. It was not always easy to capture them, for when I pushed my knife under the mouth of the gallery they moved quickly backward, and then, digging deeper into the soil, made a new gallery that branched off from the main one. It was not possible to distinguish the galleries of the crane-fly larvae from those of the other dipterous associate. Very often, from the mouth of the spiral galleries, one-third of a broken pupal skin stuck out; but larvae were found also in many of these galleries.

The imagines of the two Diptera were present in large numbers, some flying close to the ground, others resting on it. Both forms were long-legged and capable of running over the water film. I secured a pair of both in copulation. The eggs were found on the moist surface, singly or in small masses of two or three together.

The larvae feed, of course, on organic particles in the sand. The imagines were not observed to take any nourishment at all; they copulated as soon as they had left the pupal skins, and I did not find them in any other place than on the bare, moist soil where the larvae lived; not, for instance, on flowers growing near by.

A small carabid (probably *Bembidion grapii* Gyll.) was present in the locality in comparatively large numbers, evidently preying on the larvae of the Diptera. A single carabid larva also was found; from its size and habitus it may very well be the larva of the Bembidion.

A small black spider was probably feeding on the imagines of the Diptera. It did not make a regular web, but spun a number of single threads, each about two feet long, attaching them to a piece of gravel and proceeding from this as a common center, spreading the threads close to the ground like radii, and finally fastening the ends to small grains of sand.

The adult flies of *Helobia hybrida* are very common. They are the first tipulids to appear on the wing in spring, some appearing in early March or, in open winters, even in late February. They remain until late in the fall. The writer has noted the females running about on the wet sand along the banks of the Kaw River at Lawrence, Kansas, and ovipositing quite as described by Hart (1898 [1895]: 199–200).

Larva.— Length, 7.8–10 mm.
Diameter, 0.6–0.7 mm.

Coloration, pale brownish yellow.

Form moderately elongated. Body covered with a sparse appressed pubescence. Spiracular disk (Plate LXXIII, 388) surrounded by five lobes, the dorsal one notably smaller than the paired lobes; inner face of lobes with two subparallel brown lines, connected at their outer ends to form narrow V's; disk marked with about six spots between spiracles, the largest at base of ventral lobes; disk fringed with short hairs, which are interrupted for a short distance between lobes. Anal gills moderately elongated, pale. (Beling describes the three dorsal lobes of the disk as having the entire inner face shiny blackish brown, and the ventral lobes merely margined with brownish; there would thus seem to be some variation in the character and degree of markings in this species.)

Head capsule as in the tribe. Antenna with the basal segment stout, cylindrical, the apical papilla very short, subpyriform. Mandible flattened; teeth large but very bluntly rounded; apical tooth the largest, with a slightly smaller denticle on either side.

Pupa.— Length, 7–9 mm.

Cephalic crest small; lobes pointed, directed ventrad, each bearing a short, stout seta. Labrum narrow. Labial lobes large, divergent, caudal margin almost straight across. Sheaths of maxillary palpi slender, narrowed at tip (Plate LXXIII, 390). Antenna moderately angulated, ending just beyond base of wing. Pronotal breathing horns elongate-cylindrical, directed ventrad and cephalad, with rows of breathing pores along dorsal face; ventral face transversely wrinkled. Mesonotum moderately declivitous, at broad crest (Plate LXXIII, 389) armed with numerous black chitinized spines directed backward; these spines most numerous proximally, interrupted by a median space, less numerous along shoulder; four setae in a transverse row across mesonotum, two on either side of median line; lateral angle of thorax broad and blunt, with two small setae, the outermost one the larger, the inner one about half its size; an arcuated longitudinal row of about six pits extending from above axil of wing toward crest of mesonotum. Wing sheaths short, ending before tip of second abdominal segment. Leg sheaths ending opposite or slightly beyond tip of third abdominal segment; hind legs much the longest, middle legs much the shortest, fore legs intermediate (Plate LXXIII, 391).

Abdomen with a rather strong armature of stout black spines on sternal segments, on segment 3 this appearing as a small area of about ten spines, on either side of tips of hind tarsi; tergal armature much weaker or lacking; lateral spiracles very distinct, tubular, in cast pupal skin the principal tracheal trunks being very conspicuous. Female cauda (Plate LXXIII, 393) with tergal valves the longest, terminating in sharp cylindrical points; sternal valves much shorter, blunt at tips; dorsum of segment 8 with five blunt lobes. Male cauda (Plate LXXIII, 392 and 394) with dorsal valves the longest, each terminating in a long, subacute, chitinized spine directed dorsad and laterad and bearing before its tip two stout setae; ventral lobes stout and blunt, longer than dorsal lobes.

Nepionotype.— Fell, between Öraefa and Heineberg, southeastern Iceland.

Neanotype.— Cast pupal skin, with type.

Paratypes.— Numerous cast pupal skins, with types (in the collection of the Copenhagen Museum).

Genus **Trimicra** Osten Sacken (Gr. *three + small)*

1861 *Trimicra* O. S. Proc. Acad. Nat. Sci. Phila., p. 290.

Trimicra is a small genus of crane-flies, including about fifteen described species found in most parts of the world, almost all being forms of moderate size and obscure coloration. These various species bear a close resemblance to one another and are hard to distinguish specifically.

Bergroth and other European writers consider the genus Trimicra as being the same as Psiloconopa Zetterstedt, but at this time the writer is not entirely willing to accept this view.

Beling (1879:48) described what he took to be the larva of one of these flies, and in his key to the larvae of crane-flies (1886:206) he included it in close proximity to the Pediciini. As mentioned elsewhere in this paper, it is highly probable that Beling described a pediciine larva, but by an accident had larvae of Trimicra in his breeding jars, the latter larvae emerging first and confusing the author.

Gerbig (1913:161–163) describes the real larva of *Trimicra pilipes* (Fabr.), the best-known species of the genus. It is found along the margins of flowing streams with muddy banks. It is a dark-colored larva, about 15 millimeters in length and about 2 millimeters in diameter. The skin of the body is similar to that of the larvae in the typical subgenus of the genus Limnophila, being covered with chitinous, hairlike projections, which in Trimicra are longest on the dorsal surface of the body. On each segment there are solitary elongate bristles, above and below each of which is a gland. The spiracular disk (Plate LXXIII, 395) is surrounded by five nearly equal lobes, which have the inner faces marked with equal blackened, chitinized areas. On the lateral margins of each lobe, but occupying only the distal part of the lobe and not continuous around the disk, is a fringe of moderately long hairs. At the tip of each ventral lobe are two bristles, and at the tip of each lateral lobe is a single bristle, these being inserted outside the line of hairs and surrounded by a bright circular area. The ventral sensory bristles found in some crane-fly larvae (as *Tipula variipennis*) are lacking. At the base of the lateral lobes are the spiracles, which are generally similar to those in the subgenus Limnophila. Gerbig discusses in detail the structure of the spiracles, the felt chamber, and the musculation of this region of the body.

Bruch (*in litt.*) mentions the rearing of *Trimicra reciproca* (Walk.) in Argentina from larvae very similar to that described above, occurring in the same type of habitat.

Genus **Empedomorpha** Alexander (Gr. *Empeda* + *shape*)

1916 *Empedomorpha* Alex. Proc. Acad. Nat. Sci. Phila., p. 507–508.

Empedomorpha is a monotypic genus of flies, evidently related to Trimicra. It is very curious in its marked sexual dimorphism, the male having an extremely large, hairy stigma, which encroaches upon the adjoining veins and often distorts them. The fly is still very insufficiently known. It is a prairie-inhabiting species, occurring from South Dakota to Texas and New Mexico. Nothing is known concerning the immature stages, and the following observations on the habits and occurrence of the adult flies are all that are available.

Empedomorpha empedoides (Alex.)

1916 (?) *Trimicra empedoides* Alex. Can. Ent., vol. 48, p. 44–45.

Empedomorpha empedoides, as stated under the generic account above, is a prairie-inhabiting species. Adult flies were found running about on the sand flats of the Arkansas River, near Cimarron, Kansas, from July 13 to 15, 1917, by H. L. Fackler and the writer. The vegetation of the sand bars here is very sparse to almost lacking, a few psammophytic grasses being the main element. Associated with these flies on the sandy surface were a characteristic group of sand-loving insects, of which the following were the most constant: larvae and adults of tiger beetles, representing at least three species of Cicindela; ground beetles, Carabidae, including such genera as Omophron, Dyschirius, Bembidion, Tachys, and a few others; rove beetles, Staphylinidae, such as Stenus; Heteroceridae, Psammocharidae, Asilidae, Saldidae, and similar groups. In the cool of early evening, numerous small spiders that lurk in hollows and in deserted insect burrows during the day emerge from hiding and become active.

The crane-flies were observed during the hours of bright sunlight, when the temperature registered over 100° F. in the sun. They run rapidly over the moist sand, their course being very shifting and zigzag, quite like that of tiger beetles. They fly readily but only for short distances, and prefer to alight on the sand rather than on the vegetation. They walk awkwardly over the sand, but are able to crawl up grass blades or

similar objects. The habits of the adult flies are strikingly like those of Helobia (page 930). The writer is sure that the larvae are to be found in the sand in these same haunts.

Genus **Gnophomyia** Osten Sacken (Gr. *darkness* + *fly*)

1859 *Gnophomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.
1867 *Furina* Jaenn. Abhandl. Senkenb. Ges., vol. 6, p. 318.
1911 *Dasymallomyia* Brun. Rec. Indian Mus., vol. 6, p. 304.

Larva.— Body slender, tapering toward ends, with transverse welts on intermediate abdominal segments. Spiracular disk surrounded by five subequal lobes. Anal gills consisting of four blunt, rounded lobes, constructed for propulsion rather than for a respiratory function. Head capsule moderately elongated, rather compact for the Eriopterini. Antenna rather small, apical papilla elongate-oval. Mandible slender, with a long apical point and three teeth along ventral cutting edge.

Pupa.— Cephalic crest a low, blunt tubercle on either side of median line, each tipped with a long seta. Pronotal breathing horns small, narrowly trumpet-shaped. Mesonotum moderately declivitous, at crest practically unarmed; a strong seta at lateral angle of thorax and another on either side of mesonotum behind crest. Wing sheaths short, ending before tip of second abdominal segment. Leg sheaths very short, reaching just beyond wings, attaining end of second abdominal segment; all the tarsi ending about on a level. Abdomen provided with long setae; spiracles on abdominal segments 2 to 7.

Gnophomyia is a small genus including about forty described species which are most abundant in the Tropics of the New World. The European *Gnophomyia tripudians* Bergr. has recently been reared by Gamkrelidze (1913, a and b) and by Keilin (Edwards, 1919b). The former found larvae in large numbers in the viscous, semi-decomposed mass of tissue beneath the bark of a fallen carolina poplar, associated with *Miastor metraloas* Meinert. These larvae were found near Paris, France, in March, 1911. Gamkrelidze records a gregarine parasite in the intestine and a nematode worm in the body cavity. The species was later reared in England from dead oak by Keilin, who has discussed and figured glands in the larvae (1913:3). The only American species that has been reared is the common *Gnophomyia tristissima*, discussed later.

Gnophomyia rufa Hudson, of New Zealand, has recently been discussed in some detail by Hudson (1920:32–33). It is occasionally found in dense forests in the vicinity of Wellington. The larva lives in and feeds on the semi-liquid vegetable detritus which accumulates in large quantities at the bases of the leaves of *Astelia Solandri*, a common and very conspicuous epiphytic plant in most of the primitive native forests. The length of

the fully grown larva is slightly over 30 millimeters. It is subcylindrical, considerably flattened. Oval warts armed with minute teeth are situated on both surfaces of abdominal segments 2 to 7. The larva is very dark slaty gray in color, darker toward the extremities. The spiracular disk as shown by Hudson's colored figure is very small. Apparently only one larva inhabits the space between the two sheathing leaves of the Astelia, and only those leaves which are full of a thick, brown, coffee-like liquid are frequented. The pupa is inclosed in a rather tough, extremely elongate, silken tube situated between the sheathing leaves. It rests in an upright position in the midst of the semi-liquid mass. The pupa measures about 38 millimeters in length, being very elongate with the head and the thorax unusually small. The two pronotal breathing horns are shaped somewhat like a bivalve shell. Abdominal segments 3 to 6 at the base on the dorsal side have finely-toothed warts; the ventral surface has plain ridges. It is probable that the present species is not a true Gnophomyia, but until more is known of this species and its relatives it should be referred to this genus.

The *Gnophomyia pilipes* referred to by Beling (1879:42) and by Gerbig (1913:161–163) pertains to Trimicra (page 932).

G. tristissima has been recorded by Malloch (1915–17 b:230–231) as living in wet mud, but this is an error. The writer has material from exactly the same source as Malloch's, received from James A. Hyslop, and this shows that the haunt of the larvae is beneath the decaying bark of trees — an unusual habitat for one of the Eriopterini, which for the most part live in damp sand or earth near water. The rearing of this species in New York (by Young), Massachusetts (by Johnson), Maryland (by Hyslop), Virginia (by Shannon), Kansas (by Alexander), Illinois (by Malloch and Alexander), and Texas (by Mitchell), leaves no question that the immature stages are to be found beneath the decaying bark of the larger hardwood trees, the tulip tree, *Liriodendron Tulipifera* Linn., being often preferred.

Gnophomyia tristissima O. S.

1859 *Gnophomyia tristissima* O. S. Proc. Acad. Nat. Sci. Phila., p. 224.

Gnophomyia tristissima is an interesting black fly with conspicuous yellow halteres. It is common and widely distributed thruout the eastern

United States and Canada. As stated above, the species has been reared on at least seven different occasions in as many States, the most complete account being that by Hyslop, whose specimens and manuscript notes were kindly placed at the writer's disposal. His data on this species are as follows:

May 14, 1914. Wolfsville, Maryland. Under the bark of a rotten stump of a tulip poplar (Liriodendron) on the roadside near Warrenfeltz schoolhouse, field on the left going to town. I found a great number of amber-yellow dipterous larvae (three in alcohol), and also three pupae slightly shortened and with the thorax and legs ferruginous and the abdomen pale amber. They were in a very moist nidus of rotted inner bark; placed in rearing in a tin box.

May 16. One adult emerged today (pinned); pupal case in alcohol.

May 18. Three adults emerged today (pinned); pupal cases in alcohol. Observed emergence of one adult. The swaying motion observed in *Tipula infuscata* was not observed, but the adult simply glided straight out of the pupal case by a wavelike contraction of the abdomen. The whole emergence took only about eight seconds. A larva pupated.

May 23. Adult emerged. Pupal stage five days. Placed the remainder of the pupae (all had transformed from larvae to pupae) in alcohol. The pupae are quite active and move under a shelter if exposed. Just before emerging, the pupa takes on a black color on the thorax and smoky yellow on the abdomen.

Shannon's material was reared from pupae taken under the bark of a dead tulip tree at Dead Run, Fairfax County, Virginia, on May 5, 1913. A larva that is undoubtedly this same species was found beneath the same tree on April 17, 1913. Johnson bred this species from larvae found beneath bark at Riverside, Massachusetts, on April 24, 1905. The Texas specimens were found by Mitchell beneath the bark of cottonwood (Populus) at Victoria, on June 30.

At Lawrence, Kansas, in 1919, the writer found a few larvae under the bark of a box elder, associated with the following dipterous larvae: *Pterocalla strigula* Loew, *Lonchaea laticornis* Meig., *Phaonia harti* Mall. These associated species were kindly determined by Mr. Malloch. In 1920 the flies were bred from under the bark of several deciduous trees at Urbana, Illinois, by Mr. Malloch and the writer.

Well-preserved specimens of the larvae are not available to the writer, and the following description is taken direct from Malloch (1915–17 b: 230–231):

Larva.— Length, 9-11 mm. Slender, slightly tapering toward both extremities, more decidedly towards the cephalic. Body yellowish testaceous, covered with dense decumbent pile.

Head [Plate LXXIV, 396] more compact than that of Helobia, the lateral rods stouter; antennae very small; maxillae large, produced beyond the apex of the narrow labrum, the palpi stout; labium not chitinized; mandibles slender, with a long sharp apical tooth and about three poorly defined teeth along the lower lateral margin. Locomotor organs consisting of rather

broad fusiform areas on anterior portion of abdominal segments except basal and apical; hairs along margins of segmental incisions more distinct than elsewhere because of their being slightly curved upward; apical segment with five processes, their structure and markings as in figure [Plate LXXIV, 397]; anal ventral blood-gills in the form of four short rounded protuberances.

The pupa is described from four cast skins, kindly presented by Mr. Hyslop:

Pupa.— Length, 8–10 mm.

Cephalic crest a low, blunt tubercle on either side of median line, each tipped with a long, stout seta. Labrum broad, elongate, obtuse at tip, completely separating triangular labial lobes. Sheaths of maxillary palpi moderately slender, tapering gradually to tip. Antennal sheaths moderately elongated, extending to about opposite wing root; basal segments angulate. Pronotal breathing horns (Plate LXXIV, 399 and 400) small, trumpet-shaped, very flattened, median area lacking and hence the margins contiguous; just proximad of breathing horns a large, roughly triangular lobe on either side, immediately behind which are two small setae. Mesonotum moderately declivitous, at crest rather tumid, but unarmed, with a few parallel grooves on either side of median line; lateral angle of thorax very sharp, before tip with two setae, one very powerful, the more dorsal one abortive; a strong seta on either side of mesonotum behind crest. Wing sheaths short, ending just before tip of second abdominal segment. Leg sheaths (Plate LXXIV, 398) very short, ending just opposite tip of second abdominal segment and thus projecting but slightly beyond wing tips; hind legs a little the shortest, but no striking difference in length of various sheaths.

Abdominal segments subdivided into a narrow basal ring and a much broader posterior ring; abdominal segments on dorsum with four transverse rows of tiny but stout setae, two on basal ring and two on posterior ring, one being subbasal, the other subterminal, in position; sternum with only the subterminal row of setae present, but this well marked, the other rows merely vestigial; on either side of dorsum, just cephalad of ends of subterminal row of setae, a powerful bristle; in alinement with these and subequally spaced, two smaller setae; a strong pleural seta on a raised papilla opposite basal ring and three opposite posterior ring, the two anterior being larger, the posterior one very small; sternum with a strong seta on extreme lateral margin of posterior ring; lateral spiracles distinct, on segments 2 to 7. Male cauda (Plate LXXIV, 401) with ventral lobes small, blunt, rather widely separated basally but converging apically; dorsal lobes powerful, divergent, and rather acute at tips; at base of each near lateral margin a short bifid knob sending one arm dorsad, the other laterad; at base on cephalic angle a short, stout seta; two long, powerful, lateral setae on either side, and a single powerful seta on either side of dorsum, immediately behind which is a blunt tubercle. Female cauda with sternal valves elongate, powerful, at their tips terminating in slender, divergent points; dorsal valves small, blunt, divergent, located at base of sternal valves, at their tips with a short, slender spine directed backward; base of segment about as in male.

Neanotype.— Wolfsville, Maryland, May 16, 1913. No. 234.
Paratypes.— Two male and one female pupae from type locality, May 18, 1913.

Genus **Gonomyia** Meigen (Gr. *angle* + *fly*)

1818 *Gonomyia* Meig. Syst. Beschr. Zweifl. Ins., vol. 1, p. 146.
1856 *Taphrosia* Rond. Dipt. Ital. Prodr., vol. 1, p. 182.
1869 *Goniomyia* O. S. Mon. Dipt. N. Amer., part 4, p. 176.

Larva.— Form elongate, terete. Spiracular disk surrounded by five blunt lobes which are heavily marked with brown, in some species (*G. alexanderi*) the brown suffusing the disk between the spiracles. Head capsule of eriopterine type. Mandible with lateral teeth slender, flattened. Antenna with apical papilla elongate-oval. Mentum not chitinized.

Pupa.— Cephalic crest blunt, the surface with minute roughenings. Pronotal breathing horns flattened, fanlike (*G. sulphurella*), or short, trumpet-shaped. Mesonotum declivitous, at crest with an interrupted transverse row of six to eight tubercles which are densely beset with sharp black spicules. Wing sheaths attaining base of third abdominal segment. Leg sheaths moderately elongated, reaching base of fourth abdominal segment; tips of middle tarsi ending a short distance before apices of other tarsi. Armature of abdominal segments weak. Lateral spiracles distinct, tubular. Five blunt, fleshy lobes on dorsum of eighth abdominal segment.

Gonomyia is a large and diverse genus of small crane-flies (including more than one hundred known species) described from all parts of the world. They are divided into four recent subgenera, of which three — Gonomyia Meig., Progonomyia (new name for Gonomyella Alex., preoccupied), and Leiponeura Skuse — occur in the Nearctic fauna.

The immature stages of the known species are spent in moist sand or earth, usually near water. In Europe, *G. tenella* Meig. (Beling, 1879:56, mention only) was found in August in damp, sandy earth along the margin of a dried-up brook.

The writer has found the immature stages of *Gonomyia* (*Leiponeura*) *alexanderi* and *G.* (*G.*) *kansensis* in wet sand near rivers. *G. sulphurella* and *G. subcinerea* O. S. occur in muddier and more stagnant conditions near ponds and small streams.

Not enough larvae are available for study to require a key at this time. The pupae of the known Nearctic species may be distinguished by the following key:

1. Pronotal breathing horns narrow at base, expanded distally into a very flattened, fanlike blade with delicate and anastomosing nervures. . . . . . . *G. sulphurella* O. S. (p. 940)
   Pronotal breathing horns not as above, more earlike or trumpet-shaped. 2
2. Pronotal breathing horns massive, trumpet-shaped; lateral margin of thorax before wing root produced into an angle; male cauda small, elongate, dorsal lobes a little shorter than ventral lobes, with two stout lobes on dorsal side far removed from their base. . . . . *G. alexanderi* (Johns.) (p. 939)
   Pronotal breathing horns flattened, earlike or narrowly trumpet-shaped; lateral margins of thorax above wing root broad and blunt; male cauda short, stout, dorsal and ventral lobes subequal in length, the latter closely approximated along median line, the former widely separated, at their base with two acute points. . . . . *G. kansensis* Alex. (p. 941)

(Subgenus **Leiponeura** Skuse)

1889 *Leiponeura* Skuse. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, p. 795.
1915 *Lipophleps* Bergr. Psyche, vol. 22, p. 55.

Gonomyia (*Leiponeura*) *alexanderi* (Johns.)

1912 *Elliptera alexanderi* Johns. Psyche, vol. 19, p. 3.

The beautiful crane-fly *Gonomyia alexanderi* is locally common in the eastern United States. The adult flies may be swept from rank vegetation in the neighborhood of streams. When resting, the adults have a characteristic position, the fore legs standing straight ahead and almost parallel, the middle legs extended laterally and slightly forward, the hind legs directed backward but widely divergent, and the wings folded over the back. This is the characteristic resting position for the genus. The larvae were found in some numbers in rather coarse sand, around small pools of water near the Sacandaga River, Fulton County, New York, on June 5, 1914. The adults emerged on June 16, giving a pupal period of not more than eleven days and presumably much less. The description and figures of the pupa are made from the cast pupal skin of the male.

Larva.— Length, 8.3 mm.
Diameter, 0.4–0.5 mm.

Coloration very pale yellow or yellowish white.

Form terete, elongated, slender. Body with a sparse, pale pubescence, at posterior margins of segments with a transverse erect ridge of stiff hairs. Spiracular disk (Plate LXXV, 403) large, flattened, almost pentagonal in outline, surrounded by five lobes; dorso-median lobe small, slender; paired lobes very short and blunt; margin between lobes almost straight or but feebly concave; when disk is partly closed, lobes appearing a little more prominent; ventral lobes a little larger than lateral lobes; lobes heavily suffused with brown; on ventral lobes a lateral dark brown line running dorsad to near spiracles, at its dorsal end connected across disk by a paler brown suffusion; proximal stripes of ventral lobes shorter and paler, above their inner ends with a small brown spot; lateral lobes almost entirely suffused with brown, this entirely surrounding spiracles and in some specimens entirely suffusing disk between spiracles, this mark bifid at its distal end; dorsal lobe indistinctly marked with very pale brown; disk margined with short, pale hairs which are not interrupted and are only a little longer at tips of lobes. Spiracles widely separated, the distance between them being three or four times diameter of one; spiracles yellow, centers pale brown.

Head capsule as in the tribe, the ventral bars broader than the slender dorsal bars, their inner ends not expanded or toothed to form the mental plate. Labrum-epipharynx moderately elongate, densely hairy. Mentum not chitinized; hypopharyngeal region a cushion, covered with delicate, short setae. Antenna as in this tribe, basal segment moderately elongate, densely hairy, apical papilla rather small, elongate-oval. Mandible (Plate LXXV, 402)

moderately large; apical point elongated, slender; ventral cutting edge with three flattened teeth, gradually smaller from outermost toward base; outermost tooth flattened, a little enlarged distally, about as long as apical point; basal tooth small, acute; a prosthecal appendage with a brush of hairs beneath it.

Pupa.— Length of cast pupal skin, about 5.5 mm.

Cephalic crest of two prominent lobes, blunt at tips, their surface granulated. Labial lobes blunt at tips. Sheaths of maxillary palpi moderately stout, tapering suddenly to sharp apices. Antenna with basal segment very angulated. Pronotal breathing horns (Plate LXXVI, 408 and 409) massive, short, trumpet-shaped, flattened laterally, and here margined with an elevated ridge, along which are scattered the rows of breathing pores; mouth of this trumpet wide. On thorax between breathing horns, large, rounded lobes which are minutely granulated. Declivity of mesonotum (Plate LXXVI, 407) somewhat precipitous, at the rather narrow crest with about six small tubercles which are densely beset with spicules; along shoulder a similar, but more elongate, transverse welt; lateral margin of thorax before wing root projecting out as a sharp angle with a seta at its base. Wing sheaths reaching end of second abdominal segment. Leg sheaths moderately long, attaining base of fourth abdominal segment; fore legs a very little longer than hind legs; middle legs much shorter, ending just beyond base of last tarsal segment of fore legs.

Abdominal segments divided into two narrow basal rings and a much broader posterior annulus. Armature of abdomen very weak. Male cauda (Plate LXXVI, 410 and 411) small, elongate; ventral lobes a little longer than the short, blunt dorsal lobes; on dorsal face near end of eighth segment, two stout lobes pointed at the tips which are directed dorsad and slightly caudad, eighth segment with a close pentagon of pale, slender lobes, the posterior pair larger and closer together than the anterior pair, the median lobe the smallest.

Nepionotype.— Sacandaga River, Fulton County, New York, June 5, 1914.
Neanotype.— With type larva.
Paratypes.— Two larvae with type.

(Subgenus **Gonomyia** Meigen)

Gonomyia (*Gonomyia*) *sulphurella* O. S.

1859 *Gonomyia sulphurella* O. S. Proc. Acad. Nat. Sci. Phila., p. 230.
1869 *Goniomyia sulphurella* O. S. Mon. Dipt. N. Amer., part 4, p. 180-181.

Gonomyia sulphurella is a handsome little crane-fly which is very common and widely distributed thruout the eastern and central United States. Larvae are not infrequent in mud along the banks of streams. The writer has bred this species from larvae sifted from sandy mud from the banks of Cascadilla Pond, Ithaca, New York, where they occur associated with numerous larvae and pupae of a tabanid (*Chrysops indus* O. S.), a stratiomyiid (*Odontomyia* sp.), and other forms. Larvae collected on May 14, 1913, emerged as adults on June 1. Adults have been reared as late as October 19 by E. A. Richmond.

Pupa.— Length of cast pupal skin, about 6.5–7 mm.

Cephalic crest small, blunt. Labrum triangular, apex obtusely rounded. Labial lobes subcircular, outer margin rounded. Sheaths of maxillary palpi short and stout, at apex suddenly narrowed (Plate LXXVII, 414). Antennal sheaths angulated at segments, the organ extending to beyond base of wing. Pronotal breathing horns (Plate LXXVII, 413) with extreme base expanded, the neck short, constricted, soon passing into a greatly expanded and very compressed disk, the whole suggesting a fan or certain polypores; margin of this disk entire or gently crenulated, and sloping from ventral side outward; surface finely nerved and reticulated. Mesonotum somewhat precipitous, crest (Plate LXXVII, 412) tumid, with rounded knobs arranged transversely along it, there being about eight isolated knobs and a more elongate one along shoulders, these knobs covered with minute blackened spicules. Lateral margin of thorax above wing root forming almost a right angle. Wing sheaths ending opposite base of second abdominal segment. Leg sheaths comparatively short, ending opposite base of fourth abdominal segment; fore legs a little the longest, middle legs conspicuously shorter than the others.

Abdominal segments divided into two narrow basal rings and a broad posterior annulus. Armature of abdominal segments weak, posterior ring with a narrow row of small black spines before caudal margin; on basal ring a broad band of microscopic scabrous points arranged in interrupted transverse rows, there being about seven or eight of these rows to a band. Spiracles small but distinct. Female cauda with tergal valves short, but little longer than sternal valves, slightly upturned, ending in short, cylindrical tips; near base with a small, blunt tubercle on either side; dorsum of segment 8 with five rather long, pale lobes, the anterior pair more slender and more widely separated than the posterior pair, which are sometimes closely approximated.

Neanotype.— Cast pupal skin, Ithaca, New York, October 19, 1915.
Paratypes.— Three pupae with type.

Gonomyia (Gonomyia) kansensis Alex.

1918 *Gonomyia kansensis* Alex. Can. Ent., vol. 50, p. 158–160.

Gonomyia kansensis is a prairie species of the *cognatella* group and appears to be common along the Arkansas and Kaw Rivers in Kansas. Living pupae were found at Larned on August 1, 1917, in sand along the banks of the Arkansas River, where they were associated with the typical sand-loving fauna, including Gelastocoridae, Saldidae, and Carabidae (Omophron, Dyschirius, Bembidion, and Tachys). The observation of a small ant preying on a living pupa of this fly is discussed on page 729.

Pupa.— Length of cast pupal skin, 6 mm.

Similar to *G. alexanderi* in most essentials but showing the following differences: antennal sheaths strongly angulate at segments; a tubercle on ventral face of antenna at base, and another at inner cephalic margin of eye.

Pronotal breathing horns (Plate LXXVII, 415 and 416) flattened, earlike or very narrowly trumpet-shaped, with a thick marginal ridge, the disk restricted. Lateral angle of thorax above wing root very broad and blunt, setiferous. Leg sheaths of fore and hind legs almost on a level, those of middle legs shorter, ending a little beyond midlength of last tarsal segment of fore legs. Male cauda (Plate LXXVII, 417 and 418) with dorsal and ventral lobes very short and blunt, subequal in length; ventral lobes closely approximated on median line; dorsal lobes widely separated at their base, with two small acute points directed strongly dorsad, divergent at their tips, each with two small setae on outer face near base; dorsum of segment 8 with five lobes, the anterior pair a little more widely separated than the posterior pair, the median lobe slender.

Neanotype.— Larned, Kansas, August 1, 1917.

Genus **Rhabdomastix** Skuse (Gr. *rod* + *whip*)

1889 *Rhabdomastix* Skuse. Proc. Linn. Soc. N. S. Wales, ser. 2, vol. 4, p. 828–829.

The genus Rhabdomastix includes nearly a dozen species, some of which have been previously described as Gonomyiae.

The immature stages of *Rhabdomastix schistacea* (Schum.) were found by Beling (1886: 195) in wet earth beside a stream in beech woods on May 6. The larva measures 6 millimeters in length; the greatest diameter is 0.8 millimeter. The body is strongly dilated in the anterior part and gradually narrowed behind. The integument is deep brownish yellow. The spiracular disk is short and blunt, and has four very small, tuberculate teeth, the lateral pair lying somewhat more cephalad than the more powerful ventral pair; spiracles small, circular, yellowish brown, separated by a distance about equal to four times the diameter of one. The pupa has the mesonotal declivity provided with an interrupted crossrow of small, unequal, chitinized teeth.

(Subgenus **Sacandaga** Alexander)

1911 *Sacandaga* Alex. Ent. News, vol. 22, p. 349–352.

Rhabdomastix (*Sacandaga*) *flava* (Alex.)

1911 *Sacandaga flava* Alex. Ent. News, vol. 22, p. 351–352.

Rhabdomastix flava is a curious fly which is apparently related to Gonomyia but represents a quite different offshoot of the Eriopterini. The writer believes that the larvae might be found in moist earth along streams, but at present they are quite unknown. The following notes

on the swarming habits of this species have been published (Alexander, 1912 a:72–73):

On June 13, 1909, I found the species swarming [on Sport Island, in the Sacandaga River, New York] and made the following observations: The species came out at about 7.45 p.m. and at 7.51 p.m. began its flight in under an elm tree at the northeast end of the island. The flight was generally forward, but continually from side to side for a few inches. The flight was quite irregular, always toward the slight north breeze. The whole swarm would often move away and return, a little later, to the first place. It swarmed within four feet of the ground, generally much lower, averaging, perhaps, two feet. . . . The number of individuals participating in the swarm was about twenty. Other species swarming nearby at the same time were *Chironomus hyperboreus*, var. *meridionalis*, Joh., and the may-flies, *Ephemerella excrucians* Walsh, and *Siphlonisca aerodromia* Ndm.

Genus **Trentepohlia** Bigot (named after J. J. Trentepohl)

1854 *Trentepohlia* Bigot. Ann. Soc. Ent. France, p. 474.
1911 *Mongomioides* Brun. Rec. Indian Mus., vol. 6, p. 296.
1912 *Mongomella* Enderl. Zool. Jahrb., vol. 32, part 1, p. 61.

Trentepohlia is a tropicopolitan genus including about fifty-five described species arranged in six subgenera — Trentepohlia Bigot, Anchimongoma Brun., Mongoma Westw., Plesiomongoma Brun., Paramongoma Brun., and Neomongoma Alex. Of these species, fifteen are American and the remainder are Old World forms. They are almost all species of delicate, ethereal structure, with long, slender legs. It is an interesting fact that *Trentepohlia* (*Mongoma*) *pennipes* has been observed by Jacobson (De Meijere, 1911:50, and Edwards, 1912–13:211) to form chains on horizontal spider webs, as is noted herein for Thrypticomyia (page 712) and somewhat similarly for Oropeza (page 982). H. K. Munro has supplied (*in litt.*) the following interesting notes on the habits of *Trentepohlia* (*Trentepohlia*) *humeralis* Alex. as observed in eastern Transvaal at the end of April, 1920:

Very inconspicuous when flying and resting. When flying resembles very much a small piece of thistledown. Invariably settles on under side of twigs, leaves, and similar objects. Usually found among bushy undergrowth, but also in grass. When at rest the wings are folded along back; very often on settling the insect moves itself up and down in the manner of the long-legged harvest spiders (Phalangiidae). Slow flier.

A fossil Trentepohlia, *T. cruciferella* (Ckll.), has been described from the Gurnet Bay Oligocene (Cockerell, 1917b: 373–374). Observations on the immature stages of three species are available.

(Subgenus **Mongoma** Westwood)

Trentepohlia (*Mongoma*) *pennipes* (O. S.)

1887 *Mongoma pennipes* O. S. Berl. Ent. Zeit., vol. 31, part 2, p. 204.

The immature stages of *Trentepohlia pennipes* have been described by De Meijere (1911: 50–51) as follows: Jacobson found the larvae at Semerang, Java, in January, 1906, in decaying plant stems. The only larva sent was 9 millimeters long and almost 1 millimeter in diameter, of cylindrical form, only slightly narrowed behind and brownish in color. The head capsule was entirely retracted. The entire body was thickly beset with fine, short, appressed hairs; in addition to these, on the ventral side of each of the six intermediate segments were transverse swellings where the hairs were shorter and even more numerous. Surrounding the anus were four long, cylindrical, anal gills, each constricted in three or four places; if bent forward, the anterior pair would reach the middle of the penultimate segment of the body, the posterior pair being somewhat shorter. The last segment of the body was truncated, the lower angles being somewhat produced and provided with a few somewhat longer hairs; the spiracles, situated in the upper part of the spiracular field, were relatively small and somewhat elongated.

The pupa (Plate LXXVIII, 419) was about 9 millimeters long, elongate, of a yellowish brown color, the abdomen for the most part brighter. The thorax was almost smooth, with only a few short, brownish yellow bristles. The abdomen, except on the anterior segments, was thickly set with numerous tubercles. The apex of the abdomen had two short, thornlike projections, curved outwardly; beneath these were two shorter tubercles, and four short tubercles formed a quadrangle on the dorsum of the last segment. The pronotal breathing horns consisted of flattened, leaflike lobes, the upper surface of which was scaly.

(Subgenus **Paramongoma** Brunetti)

Trentepohlia (*Paramongoma*) *bromeliadicola* (Alex.)

1912 *Mongoma bromeliadicola* Alex. Ent. News, vol. 23, p. 415–417.

Trentepohlia bromeliadicola and *T. leucoxena* have a larval habitat which has not been found elsewhere in the family. They live in the water that gathers in the leaf axils of tropical bromeliaceous plants,

spending their immature stages in this habitat, where they are associated with a remarkable fauna of other organisms. The adult females have the valves of the ovipositor greatly elongated, and the writer has suggested elsewhere that this may be an adaptation for laying the eggs in this habitat. *T. bromeliadicola* was reared in Costa Rica by Picado, whose important paper (Picado, 1913) on the bromeliaceous epiphytes contains colored figures of the larva, the pupa, and the adult. From this paper it is seen that the larva (page 356, figure A, and plate 13, figure 4, of reference cited) is not unlike that of *T. pennipes*, described above, the four prominent anal gills of *T. bromeliadicola* (Plate LXXVIII, 420, of this paper) being a notable feature in common, altho here the constrictions are very numerous, there being twenty-five or thirty shown in the figure. The pupa (Picado, 1913:357, fig. 51, and pl. 13, fig. 2) has the pronotal breathing horns (Plate LXXVIII, 421, of this paper) approximated on the median line, and the sheaths of the ovipositor (Plate LXXVIII, 423) greatly elongated to contain the elongated terebra of the adult within. According to Keilin (1913), the tegumentary glands of this larva are a provision against drought, which is the great source of danger to organisms living in this habitat.

Trentepohlia (*Paramongoma*) *leucoxena* (Alex.)

1915 *Mongoma leucoxena* Alex. Ent. News, vol. 26, p. 29–30.

Trentepohlia leucoxena was reared by Knab in Mexico, from larvae found living in bromeliaceous plants quite as in the preceding species.

Genus **Teucholabis** Osten Sacken (Gr. *weapons* + *forceps*)

1859 *Teucholabis* O. S. Proc. Acad. Nat. Sci. Phila., p. 222.

Larva.— Form elongate, slender, terete. Body practically destitute of pubescence and setae. Spiracular disk surrounded by three very broad lobes, a flattened ventral lobe and two shorter lateral lobes at the base of which are the small black spiracles. Gills four, bluntly rounded and developed for propulsion. Head capsule of four elongate, slender rods or plates, interno-lateral pair forked at about midlength. Mandible rather small, with about three blunt lateral teeth. Antenna elongate, two-segmented.

Pupa.— Cephalic crest setiferous. Pronotal breathing horns short, blunt, closely applied to thorax. Mesonotum precipitous, at crest with two powerful hooks and smaller serrated plates near shoulder. Wing sheaths reaching end of second abdominal segment. Leg sheaths reaching end of fourth abdominal segment, middle tarsi the shortest. Abdomen with a transverse row of setae before ends of segments.

Teucholabis is a rather extensive genus of small crane-flies (including more than fifty described species) which find their center of distribution in the Tropics of the New World. A few species occur in Africa and the Oriental region. The genotype, *Teucholabis complexa*, is the only species that has been reared (Johnson, 1900). Johnson's material was kindly sent to the writer for study, and furnishes the basis for the following descriptions.

Teucholabis complexa O. S.

1859 *Teucholabis complexa* O. S. Proc. Acad. Nat. Sci. Phila., p. 223.

Larvae of *Teucholabis complexa* were found by Johnson in considerable numbers beneath the bark of a decayed oak below Avalon, New Jersey, on June 8, 1899. They commenced pupating about the 13th, the imagines continuing to emerge from the 22d to the 27th. This gives a pupal duration of not more than nine days.

Larva.— Length, 9 mm.
Diameter, 0.55–0.6 mm.

Coloration pale yellowish white, spiracles conspicuously darker.

Form long and slender, body terete, tapering abruptly to the small prothoracic segment (Plate LXXIX, 424). Sutures between segments indistinct. Body practically destitute of pubescence and setae. Spiracular disk (Plate LXXIX, 427) with a broad, flattened, ventral lobe, which is very bluntly rounded to subtruncate at apex, and two very short, blunt, lateral lobes, at the base of which are the spiracles; spiracular disk without distinct markings. Spiracles small; middle piece black, ring pale horn-color; spiracles rather widely separated, the distance between them about equal to the long diameter of one. Anal gills (Plate LXXIX, 428) represented by four blunt, rounded lobes, which are apparently developed for propulsion rather than for a respiratory function.

Head not easily distinguishable in material available for study. Head capsule consisting of four long, slender, rodlike plates, the internal lateral pair forked at about midlength, so that capsule ends in six rods. Epipharynx with numerous small spines. Antenna (Plate LXXIX, 426) two-segmented, basal segment elongate-cylindrical, apical segment small, ovate. Mandible (Plate LXXIX, 425) rather small, apical point inconspicuous, with about three similar lateral teeth below it. Lobes of the maxilla blunt, stout, hairy, not extending far beyond tip of mandible.

Pupa.— Length, 6.5–6.6 mm.
Width, d.-s., 1–1.1 mm.
Depth, d.-v., 1.2 mm.

Coloration pale; head, thorax, and sheaths of appendages darker; eyes black.

Form slender, narrowed behind. Between antennal bases a prominent, two-parted crest, each lobe somewhat truncated behind and bearing a single stout seta. Front above eyes

slightly raised, two narrow lines on front, meeting below at a very acute angle. Eyes large in male, smaller in female, the front correspondingly narrowed or broadened. Labrum short, subtriangular. Sheaths of labial lobes small, suboval, separated by tip of labrum. Sheaths of maxillary palpi short, stout, straight. Antennal sheaths moderately long, extending to just beyond wing base; basal segments prominent, indicated on sheath as prominent elevations. Pronotal breathing horns short, blunt, anterior face closely applied to pronotum, outer face free; at base a small rounded knob. Thorax very deep, precipitous, at crest (Plate LXXIX, 429) armed with two strong curved hooks, one on either side of median line; on shoulder laterad of these hooks, two prominent flattened plates whose margins are minutely serrated, the dorsal, or outer, plate being the larger and terminating in a large curved hook. Wing sheaths moderately broad, ending just before tip of second abdominal segment. Leg sheaths (Plate LXXIX, 430) long and slender, outer pair much the longest, ending about opposite tip of fourth abdominal segment, middle pair the shortest. Mesonotum with two strong setae.

Abdominal segments divided into two annuli by an indistinct suture, anterior ring narrow; anterior ring with a strong seta on pleural region; posterior ring with strong setae on dorsum and sternum near caudal margin; three other setae on pleural region, two at about midlength of segment, the third near base and more dorsal in position. Male cauda (Plate LXXIX, 431) suddenly narrowed, terminating in two blunt ventral lobes and two acutely pointed dorsal lobes bent strongly dorsad at their tips and bearing a short seta in notch on inner face before apex; near base of cauda, on dorsum, a broad transverse swelling terminating in two widely separated, slender tubercles, immediately cephalad and laterad of which is a long seta; three strong setae on either side near base of cauda; posterior margin of segment 7 with two powerful, decussate setae on dorsum, and between them two small setae; another powerful seta near pleural region, and just inside still another smaller seta.

Nepionotype.— Avalon, New Jersey, June 8, 1899.
Neanotype.— With type, June 14, 1899.
Paratypes.— One larva and one pupa.

Genus **Cladura** Osten Sacken (Gr. *branch* + *tail*)

1859 *Cladura* O. S. Proc. Acad. Nat. Sci. Phila., p. 229.

The genus Cladura includes six known species — two from eastern North America, one from western North America, and three from Japan. The small *Cladura delicatula* Alex., of the mountainous regions of the northeastern United States, differs from the genotype, *C. flavoferruginea* O. S., in several important respects and it is necessary to erect a new group to receive it. This group may, for the present at least, be considered as a subgenus of Cladura, and the name *Neocladura* (Gr. *new* + *Cladura*) is proposed. Moreover, the genera Crypteria Bergr. and Pterochionea Alex. are closely related to Cladura, and the entire group are almost certainly the direct forbears of the subapterous genus Chionea Dalman. Neocladura

curiously combines the structural characters of Cladura, Pterochionea, and Crypteria. In the long basal fusion-segment of the antennal flagellum and in the wing venation, it agrees with Pterochionea and, to a somewhat lesser degree, with Cladura. In the structure of the male hypopygium, which has two slender pleural appendages, it departs widely from the type of typical Cladura, Chionea, and Pterochionea, and agrees better with Crypteria, as well as with Conosia v. d. W. and Lecteria O. S. Because of this combination of characters, Neocladura must be separated in some manner from Cladura in the strict sense. It must be borne in mind, however, that the conspicuous difference in the structure of the male hypopygium probably has a phylogenetic significance, and the two flies may not be so closely united as this arrangement would indicate.

The habits of the adult flies of Cladura and Neocladura are generally similar. Both species fly in late summer and in the autumn. They often occur on dry, wooded hillsides remote from streams and other bodies of water. The habits of the adult flies of *Cladura flavoferruginea* have been discussed by the writer in an earlier paper (Alexander, 1910:250, as *C. indivisa*). His observations, made near Gloversville, New York, on September 22, 1909, are as follows:

I went to Simmon's Woods, southeast of Gloversville, New York, this afternoon, and was very agreeably surprised at the occurrence, in large numbers, of this usually uncommon insect. Near the entrance of the woods, where Simmon's Brook emerges, the insects were found in numbers. At each step they flew out of the bushes to others farther away. They are wary insects, and when sitting on the upper side of a leaf, slip over the edge and hang inverted from the lower side when alarmed by an observer. They present a very characteristic attitude, sitting on the leaf of a tree, with their wings folded flat over the abdomen, and the six long legs stretched out over the leaf. A few were taken in copulation; these were all hanging on the under side of a leaf. Their habit of clinging to the under surface of a leaf is quite remarkable and I found several by looking for them there.

There were hundreds of specimens in the low bushes of the woods, usually on the broad leaves of deciduous trees at a height of two or three feet. Sometimes they would alight on hemlock, and, occasionally, in ferns near the ground. It was the only tipulid observed here to-day.

The eggs of *C. delicatula* have been taken from gravid females. They are comparatively few in number, but because of their unusual size they almost fill the entire abdominal cavity of the fly. These large eggs are elongate-ovate in shape.

Cladura flavoferruginea O. S.

1859 *Cladura flavoferruginea* O. S. Proc. Acad. Nat. Sci. Phila., pl. 4, fig. 34.
1861 *Cladura indivisa* O. S. Proc. Acad. Nat. Sci. Phila., p. 291.

The immature stages of *Cladura flavoferruginea* were discovered while this paper was in press. A brief account of the larvae and pupae are given here in order to complete the data.

The larvae were found in Augurville Woods near Urbana, Illinois. They occurred in soil which was baked hard and dry and which supported scarcely any other insect life. Associated with the larvae when first discovered were larvae of a scarabaeid, *Xyloryctes satyrus*; a tenebrionid, *Meracantha contracta*; a few dipterous larvae of the genera Sciara and Psilocephala; millepedes of the genus Spirobolus; and a few less common forms of animal life. A layer of dead leaves and other decaying vegetable matter covered the surface, but this had not prevented an almost complete drying out of the soil to a depth varying from six inches to more than a foot. The only other tipulid larvae characteristic of such dry soil are species of Dicranoptycha (page 828).

The most conspicuous features of the pupa are its exceedingly small size as compared with the adult fly that emerges from it, and the entire lack of protuberant pronotal breathing horns.

Larva.— Length, 10–10.5 mm.
Diameter, 1.2 mm.

Coloration light yellow thruout.

Form comparatively short and stout. Integument provided with a delicate appressed pubescence; no distinct setae. Basal annulus of abdominal segments 2 to 7 with a transverse area of microscopic points arranged in long transverse rows; last ventral segment with a flattened lobe covered with short setae, evidently an organ for shoving. Spiracular disk entirely without lobes, the spiracles being located on the exposed dorso-caudal surface of the last abdominal segment. Head capsule relatively compact; frontal plate broad, only slightly narrowed behind. Labrum quadrate, with conspicuous oval lateral arms. Antenna two-segmented, terminal segment elongate-oval. Mandibles of a herbivorous type, with an apical point and two incomplete rows of teeth on inner, or cutting, face. Mental bars widely separated, each bar provided with two acute teeth at its proximal end.

Pupa.— Length, 6.7 mm.
Width, 1.4 mm.
Depth, 1.4 mm.

Coloration pale yellow; head, thorax, and appendages darkening in age.

Cephalic crest gibbous, entire or feebly bifid, armed on either side with a single powerful bristle; two bristles on vertex and two on front; labrum with a pair of small bristles at each cephalic lateral angle. Labial lobes subquadrate, weakly separated by apex of labral sheath. Palpal sheaths short and stout, straight. Lateral margin of eye produced laterad into a digitiform lobe. Antennal sheaths extending to opposite one-third length of wing sheaths. Pronotal breathing pores entirely sessile. Pronotum and mesonotum armed with

conspicuous bristles. Wing sheaths ending opposite base of third abdominal segment. Leg sheaths unusually long, ending opposite base of sixth abdominal segment; hind legs the longest, middle legs the shortest. Abdominal tergites with ten strong bristles, eight being arranged in a single transverse row along posterior margin; abdominal pleurites with four strong bristles, one on each anterior ring, two near caudal margin of posterior ring, one ventrad of spiracle, the last-named rudimentary, located on segments 2 to 7; sternites unarmed with bristles.

Genus **Chionea** Dalman (Gr. *snow*)

1816 *Chionea* Dalm. K. Vet. Akad. Handl., vol. 1, p. 102.
1912 *Sphæconophilus* Beck. Ann. Soc. Ent. Belgique, vol. 56, p. 142.

Chionea is a small genus of nearly apterous crane-flies, found thruout the North Temperate Zone. All of the known species (about eight) have the wings reduced to mere vestiges, this being the only genus of considerable size in which all the species show this condition. The South African genus Platylimnobia Alex., which shows a somewhat similar condition of wing atrophy, is probably not very closely allied to Chionea.

The adult flies of Chionea are most often found walking awkwardly over the snow in the late fall or early spring or during warm days in winter. A few instances, however, have been recorded in which specimens were found with the temperature below freezing. At other seasons of the year they may be found among fallen leaves, under moss and stones, in the nests of small mammals as Arvicola (Schmitz, 1914), or in deserted subterranean wasps' nests (Schmitz, 1916, and Becker, 1912). Interesting accounts of the habits of the adult flies of the commonest local species, *Chionea valga* Harris, are supplied by Ainslie (1906), Johnson (1907), Washburn (1907), and others. Lugger (1896) gives the following interesting account of the habits of the same species:

> As a general rule the wingless flies are found only early in the morning, though in one case a female was discovered crawling over the snow in the evening. . . . A few winters ago the writer discovered a female moving slowly over the snow and by searching he soon detected a male. Putting both together under an inverted glass the snow-flies immediately mated, notwithstanding it was several degrees below the freezing point. Soon afterward the female found a crack in the glassy surface of the frozen snow, and forcing herself into it slowly disappeared from view. Penetrating for some depth into the snow she deposited a number of elongated eggs, which, however, did not hatch. Most females found seemed to have the eggs already fully matured and only lacked to be fertilized.

Frauenfeld (Brauer, Egger, and Frauenfeld, 1854:616) believed that the eggs are deposited in snow, since they are often laid in January or February. He thought the slimy substance secreted by the small lateral

vesicles of the *receptaculum seminis* of the female acts as a covering to protect the eggs from wet and cold. It seems probable, however, that the flies enter some crevice in the snow around the base of trees or shrubs and reach solid earth, at least in some cases. Many authors have held the flies to be nocturnal in their habits. Recently, Marchand (1917) has furnished some interesting notes on an alpine Chionea, presumably *C. alpina* Bezzi. His observations and experiments showed him that Chionea was perfectly adapted to life on the snow, being attracted to this medium by its bright light and white color, the contact of the cold surface on the feet resulting in a direct stimulus thru the claws. The insects drink water by pressing their proboscides against the snow. Marchand considers the principal reason for these activities' being held on the snow to be for the purpose of mating, since the insects can cover considerable distances over the level surfaces and are much more visible to one another at this time. The copulation of this crane-fly has been fully described by Mik (Osten Sacken, 1887:196) as follows:

> The upper valves of the ovipositor prevent the male from getting on the back of the female; it lies on its own back, in the direction of the longitudinal axis of the body of the female; when the latter is walking it drags the male, who raises himself on his hind legs to an almost perpendicular position; this serves to explain the unusual incrassation of these legs.

The genotype, *C. araneoides* Dalm., is the only species whose immature stages have been described.

Chionea araneoides Dalm.

1816 *Chionea araneoides* Dalm. K. Vet. Akad. Handl., vol. 1, p. 104.

The present knowledge of the life history of *Chionea araneoides* is due almost entirely to the work of Brauer, Egger, and Frauenfeld (1854). In February these investigators brought living adults, taken in copula, into an unheated room and placed them with their natural surroundings, such as rich, damp, humous earth, rotten grape leaves, and similar substances, in glass containers. After a time a great number of small, elongated eggs of a hyaline appearance were noted, laid at random, some being deposited on the walls of the container, where they adhered but soon shrunk and appeared dried out. Unfortunately the duration of the egg stage was not ascertained. Some weeks later the young larvae were found in the soil. They were of a cylindrical form, very pale yellow in color and not especially active. They were associated with numerous

larvae of *Sciara longipes* Meig. Toward the end of May only a few larvae were left, and these appeared fully grown but were not carried over into the pupal condition, which is still unknown.

Larva.— Length when fully grown, 7.4 mm.

Color light reddish yellow, contents of alimentary tract showing thru body. Body terete (Plate LXXXII, 443), consisting of twelve segments, there being, besides the head, three thoracic and nine abdominal segments; last segment wedge-shaped (Plate LXXXII, 446 and 447), obliquely truncated so that the surface slopes from behind upward. Two spiracles on this oblique surface, with a paler brown, pincer-shaped mark between. Mouth parts powerfully constructed. Mandible (Plate LXXXII, 444), produced into a long apical point; near midlength on inner edge of mandible a deep incision, distad of this about five teeth, basad of it three teeth. Labrum quadrangular, with two lateral points on anterior part. Mentum projecting outward as a cuticular rounded lobe. (Brauer shows two other appendages which are toothed on the outer face [Plate LXXXII, 445, of this paper]; these probably represent part of the mentum, but from Brauer's figures they would appear to lie above the labrum.)

Subtribe **Elephantomyaria**

Genus **Elephantomyia** Osten Sacken (Gr. *elephant* + *fly*)

1859 *Elephantomyia* O. S. Proc. Acad. Nat. Sci. Phila., p. 220.

Larva.— Form terete. Segments of body just before sutures with transverse rows of stiff hairs; abdominal segments 5 to 8 on ventral surface with a mouthlike depression surrounded by long, stiff hairs. Spiracular disk surrounded by four lobes, ventral pair the longest, each of the latter bearing at its tip a single very long bristle. Spiracles moderately large, located at base of lateral lobes. Head capsule very long and narrow, the four plates very elongated. Mandible very small. Maxillary palpi short. Esophageal region surrounded by chitinized plates which are conspicuously obliquely ridged. Body of larva covered with numerous long, appressed hairs, producing a satiny appearance. Coloration saturated golden yellow.

Pupa.— Form slender. A small crest on vertex above eyes. Eyes very large, globular, narrowly separated on frontal and vertical regions. Rostral sheath very elongated; palpi recurved against it. Antennal sheaths lying across eye. Head and thorax with setiferous tubercles. Abdomen with rudimentary lateral spiracles.

Elephantomyia is a small genus of crane-flies including about a dozen described living species. These are found in widely separated regions of the world, there being about four in the East Indies, five in Africa, and two in North America, one of which has been recorded also from Europe. The genus is found fossil in the Baltic amber. The adult flies are remarkable for their very elongated rostra, and undoubtedly they feed on the nectar of tubular flowers as in the related genus Toxor-

hina. No records are available, however, to indicate what species of plants are thus frequented. The larvae live in decaying wood. The only species whose immature stages are known is the genotype, *Elephantomyia westwoodi*. The literature on the immature stages of this group of flies is very limited, the only record being the unknown Limnobiine No. 1 of Malloch (1915–17 b:235–236), who gives a good description of the larva. The pupa is here described and figured for the first time.

Elephantomyia westwoodi O. S.

1869 *Elephantomyia westwoodi* O. S. Mon. Dipt. N. Amer., part 4, p. 109.

Elephantomyia westwoodi is a rather common fly in eastern North America. The adults are usually found in cool, shaded woods and may be swept from vegetation in these localities. The larva lives in decaying wood, as is shown by the three records available to the writer.

The larvae were found by Shannon in a very wet, rotten, willow log lying near the tidal flat above the brewery at Rosslyn, Virginia, on May 21, 1913. About eight larvae were found, well scattered thru the log. They were very active in their movements and were very beautiful, in life being of a deep golden yellow color. These larvae were placed in rearing, and adults issued on May 27 and 29 and June 5 and 7, indicating a pupal duration of a week or slightly less. Larvae were found in this log also on November 23, 1912, and at that time they were almost grown, being about one-half inch in length. This shows that the species spends the winter as almost fully grown larvae.

Johnson found these larvae near Edge Hill, Pennsylvania, on June 25, 1899, and on May 25, 1905, in a log, just beneath the bark. Larvae and pupae obtained by him were in the material studied in the preparation of this paper.

Malloch found a single larva of this species in a much decayed log at White Heath, Illinois, on April 30, 1916 (Malloch, 1915–17 b:236).

Larva.— Length, 10–13.4 mm.
Diameter, 1.2–1.3 mm.

Coloration of body, a deep saturated golden yellow thruout.

Body moderately elongated, terete, relatively slender, tapering gradually toward either end but more noticeably and abruptly toward anterior end (Plate LXXX, 432); the three thoracic segments gradually increasing in size from the prothoracic backward. Abdominal segments 1 and 2 short, the third to the fifth the longest, remaining segments gradually shorter. Sur-

face of body densely covered with long, satiny, appressed hairs; thoracic and abdominal segments with a dorsal and a ventral transverse ridge of short, stiff hairs just before caudal margins of segments, these being longest on lateral parts of ridge; dorsal segments 6 and 7 with incomplete transverse rows at about midlength; on ventral surface of abdominal segments 1 to 3, near base, two transverse rows of tiny spines with a depressed area between; segment 4 without this distinct double ridge; segments 5 to 7 with a very conspicuous mouthlike depression at base of each, with a liplike margin on either side, the anterior margin narrow with stiff hairs, the posterior margin swollen and densely set with tiny spines; on segment 8 the transverse mouth lying near end of segment, its anterior lip with a dense fringe of long hairs directed backward. Spiracular disk (Plate LXXX, 434) surrounded by four lobes; lateral lobes the shortest, blunt at tips, inner face of each lobe slightly expanded at tip, a few short silky hairs on outer face of lobe, inner face slightly chitinized; ventral lobes longer, broad, tapering gradually to obtuse tips, notch between lobes deep, V-shaped, a narrow fringe of short, dense, golden, recurved hairs along outer face; at tip of each ventral lobe a single long, powerful bristle. Spiracular disk unmarked. Spiracles large, very widely separated, situated at base of lateral lobes.

Head capsule (Plate LXXX, 433) very small and narrow, the plates, four in number, being greatly elongated. (The exact details are difficult to see in the material available for study.) Labrum broad, anterior margin evenly rounded, with a few long hairs. Epipharyngeal region provided with long setae directed backward. Mandible very small, base narrowed, tip produced into an acute point with smaller teeth at about midlength. Mental region feebly chitinized. Hypopharynx semicircular, rounded, anterior margin delicately grooved. Esophageal region elongated, inclosed by chitinized plates provided with parallel ridges running outward on one side and inward on opposite face, upon focusing producing a latticed appearance. Maxilla densely hairy. Antenna two-segmented, conspicuous; basal segment short, apical segment larger, suboval. Sides of capsule on swelling behind the maxilla with a brush of very long hairs. Plates of capsule elongated, expanded and chitinized at tips and along margins; ventral plate near esophageal region with setae.

Pupa.— Length, 8.4 mm.
Width, d.-s., 1.1 mm.
Depth, d.-v., 1.3 mm.

Coloration light yellowish brown; abdomen darker; thoracic dorsum, sheaths of legs, and ovipositor more yellowish. (In younger pupae the coloration is more uniformly pale.)

Form slender, body narrow. Eyes very large, rounded (Plate LXXXI, 441). Antennal sheaths lying directly across face of eye. Vertex with a small but prominent crest lying transversely above eyes; cephalad of this crest and just proximad of the antennal bases, a setiferous tubercle. Front between eyes moderately broad, produced caudad into the very elongate rostral sheath, which is transversely wrinkled. Sheaths of maxillary palpi recurved, lying alongside rostrum. Sheaths of labium tiny, bilobed, lying at tip of rostrum. Two long setae on front between eyes. Eyes very large, narrowly separated on dorsum of head, the hinder part sunken under pronotum. Two conspicuous black tubercles behind antennal bases, each bearing a long, stout seta. Pronotal breathing horns (Plate LXXX, 435) small,

short, clavate, yellow, constricted at bases, which are blackened; a prominent seta just above each breathing horn; two setae on each side of pronotum beneath eye. Mesonotal prescutum strongly convex, with six strong setae on each side, one just cephalad of base of wing, another at joint of wing, and two semitransverse groups in front of and behind level of wing base. Wing sheaths short, ending some distance beyond tips of hind tibiae and just beyond base of third abdominal segment. Leg sheaths (Plate LXXXI, 442) with fore femora strongly swollen, lying alongside rostral sheath; tips of middle tibiae ending just beyond tips of fore tibiae; legs very long, ending just before tip of fifth abdominal segment.

Abdominal segments densely and microscopically punctulate. Segments 2 to 7 with two narrow basal rings and a broad posterior ring. Setae of dorsal abdominal segments (Plate LXXX, 437) on the posterior ring consisting of a caudal series of two strong outer setae and two smaller inner ones, the outer one of the inner series close to the proximal one of the outer series; lateral series of setae powerful; basal series in alinement with anterior lateral seta, consisting of two powerful outer setae and a delicate inner one; pleural segments with a rudimentary spiracle on segments 2 to 7, each spiracle with a stout seta above it; setae of ventral segments (Plate LXXX, 436) with two strong bristles on each side near posterior lateral margin, the outermost with a tiny seta above it; a single basal seta located on a level with vestigial spiracles. Female cauda (Plate LXXX, 439) with sternum of eighth segment having two sharp, curved, widely separated spines, and just laterad of these a stout seta; pleural region with another seta on same level; sternal valves of ovipositor only a little shorter than tergal valves; dorsum of segment 8 with two long teeth, above which are two slender, divergent tubercles; tergal valves broad basally, narrowed suddenly at tip, on either side with a small, subapical seta. Male cauda (Plate LXXX, 438 and 440) with eighth sternite having a strong median tubercle that is two-toothed; laterad of this a strong chitinized tooth bearing a powerful seta on outer face; a similar strong lateral seta; eighth tergite with four strong tubercles arranged to form a square; ninth sternite blunt, each lobe ending in two small tubercles; ninth tergite ending in two divergent lobes bearing at tip a large and a small seta and on dorsal face at about midlength another strong seta.

Nepionotype.— Rosslyn, Virginia, May 21, 1913.
Neanotype.— Edge Hill, Pennsylvania, May 25, 1905.
Paratypes.— Larvae with type larva (two) and with type pupa (two).

Genus **Toxorhina** Loew (Gr. *bow* + *nose*)

1835 *Limnobiorhynchus* Westw. Ann. Soc. Ent. France, p. 683 (spurious name).
1851 *Toxorhina* Loew. Linnaea Entomol., vol. 5, p. 400.
1869 *Toxorrhina* O. S. Mon. Dipt. N. Amer., part 4, p. 109–114.
1910 *Neoceratocheilus* Wesché. Journ. Linn. Soc., Zool., vol. 30, p. 358.

Toxorhina is a small genus including about nine described species, almost all of which are from the New World. Two species occur in Africa and one in India. *Toxorhina madagascariensis* Meun. is described from African copal (Pleistocene). Nothing has been published concerning the immature stages of any member of this genus.

Toxorhina muliebris (O. S.)

1865 *Toxorrhina muliebris* O. S. Proc. Ent. Soc. Phila., p. 233.

Toxorhina muliebris is the commonest species of the genus in the United States, with a rather wide range thruout the Northeastern States. The adult flies suck nectar from various flowers, such as the following: Rhamnaceae, *Ceanothus americanus* Linn. (Banks); Ericaceae, *Clethra alnifolia* Linn. (McAtee); Apocynaceae, *Apocynum medium* Greene (McAtee); Compositae, *Solidago canadensis* Linn. (Knab).

The immature stages are unknown, but from Mrs. Tothill's tent-trap observations they are presumably spent in mud, since adult flies were found in her traps set over wet, sedgy spots near Ithaca, New York. It may be, however, that the insects live in fragments of decaying wood which might be buried in this mud, since such a habitat conforms more closely to that of Elephantomyia, which is apparently closely related to Toxorhina.

Eriopterine No. 1

A very curious larva, which has not been reared, has been found in various places near Ithaca during the past few years. It is a small, pale larva, very delicate and almost diaphanous in appearance, at the posterior end with five flattened black plates with serrated margins, and with its thoracic segments capable of considerable lateral extension. The larva is undoubtedly an eriopterine, but it introduces a type of spiracular disk that has not been found elsewhere in the tribe. The writer finds it difficult to believe that this curious larva can belong to any of the eriopterine genera discussed in this paper, and yet there are very few possibilities remaining; and one of these (Cryptolabis) does not occur in the habitat frequented by this larva. The genus Atarba, whose immature stages are still wholly unknown, is a possibility. Empeda, which the writer considers to be a subgenus of Erioptera, has not been reared and must also be considered as a possibility. If this is the larva of Empeda, the group at once assumes full generic rank as given it by Osten Sacken, but occupying an isolated position and no closer to Gonomyia than to Erioptera. The larvae of this species were found commonly on Bool's hillside, at Ithaca, where they occurred in association with numerous other crane-fly larvae discussed elsewhere (page 781). The

larva is described here in the hope that it will be reared and its identity ascertained.

Larva.— Length, 7–8.2 mm.
Diameter, 0.4–0.5 mm.

Coloration pale yellowish white; skin very delicate, almost diaphanous.

Body moderately elongated, terete; meso- and metathoracic segments (Plate LXXV, 404) and eighth abdominal segment capable of considerable expansion laterally, and, in death, usually greatly swollen; last segment of body narrowed, cylindrical, with a number of long setae, including a group of five near base of lateral lobes. A few scattered setae along abdominal segments. Spiracular disk (Plate LXXV, 405) surrounded by five equal elongate spatulate blades, these blades flattened, jet-black in color, margins finely toothed; paired lobes near base with a subhyaline median spot; margins of lobes (Plate LXXV, 406) with twenty-five to thirty hooks, recurved ones alternating with others laterally directed; when blades are closed, these margins hooking closely together; at ends of blades and sparsely scattered along margin, long, delicate setae; at apex of blades, two bristles; no spiracles found at base of lobes. Anal gills four, lateral pair elongated, telescopic, inner pair shorter.

Head capsule much as in other eriopterine genera, especially Ormosia and Gonomyia, dorsal plates slender, ventral bars a little longer. Labrum as in the tribe; epipharyngeal region with a large apical setiferous pad and two smaller pads nearer base. Mentum not formed of ventral bars of capsule as in Molophilus. Hypopharynx a semicircular cushion covered with long, dense setae, their tips a little recurved. Antenna with apical papilla very long for this tribe, about equal in length to basal segment, cylindrical, with tip rounded. Mandible moderately large, apical tooth not prominent, lateral teeth rather conspicuous, basal ones smaller but not so excessively reduced as in other members of the tribe; prostheca large.

(Described from larvae, Ithaca, New York, May 11, 1917. No. 29–1917.)

Tribe Styringomyiini

The Styringomyiini comprise a small group of very peculiar crane-flies with a tropicopolitan distribution. There is only the single genus, Styringomyia, with about twenty-five described species. Most of the species are from tropical Africa and Asia, tho a few range into Australia and the Hawaiian Islands, and one, *Styringomyia americana* Alex., is found in tropical South America.

Genus **Styringomyia** Loew (Gr. *a kind of tree-gum + fly*)

1845 *Styringomyia* Loew. Dipt. Beitr., vol. 1, p. 6. (Correctly *Syringomyia* — Bergroth *in litt.*)
1903 *Idiophlebia* Grünb. Zool. Anzeig., vol. 26, p. 524–528.
1912 *Pycnocrepis* Enderl. Zool. Jahrb., vol. 32, part 1, p. 65.
1917 *Mesomyites* Ckll. Proc. U. S. Nat. Mus., vol. 52, p. 377.

The history of the genus Styringomyia is remarkable. It was erected by Loew in 1845, being based on the fossil species *Styringomyia venusta* Loew, from African copal. Many years later it was found to be still living in the Tropics of both hemispheres. The earliest fossil records pertain to the Oligocene of northern Europe (page 765).

The adult flies have such a curious structure that it seems best to remove them from the former tribe Antochini, where they have long been placed. Concerning the first living species to be described, the Hawaiian *S. didyma* Grimsh., Perkins (1913: clxxxii) says:

> It sometimes swarms at night around the electric lights, sitting quietly on the walls and ceilings, with the body pressed closely to the surface, and the front and middle legs extended straight forward in front of the head in a characteristic manner.

Annandale has made similar observations on the resting positions of *S. ceylonica* Edw., taken in India. He says (cited by Edwards, 1914–15: 207): "This species rests on walls with the two anterior pairs of legs stretched out straight in front and the posterior pair behind, resembling a stray piece of cobweb." Jacobson has recorded much the same for *S. jacobsoni* Edw. (De Meijere, 1911: 41–42, as *S. didyma*) in Java. The flies are attracted to lamps and are almost always to be found in copulation, the head of one directed away from the other; while thus engaged, sometimes one, sometimes the other, will run forward for a short distance, producing a peculiar appearance. Munro (*in litt.*) reports that the habits of *S. vittata* Edw. as observed in eastern Transvaal in late April, 1920, are very similar. He writes: "Two specimens taken 'in cop.' Settled on under side of a twig, heads in opposite directions, front legs of each stretched out in front along twig, wings laid flat along abdomen."

Styringomyia didyma Grimsh.

1901 *Styringomyia didyma* Grimsh. Fauna Hawaiiensis, p. 10.

In *Fauna Hawaiiensis*, Perkins (1913: clxxxii) mentions the breeding of *Styringomyia didyma* by F. W. Terry. Before the reference could be investigated by the writer, Mr. Terry died. The following letters from O. H. Swezey in regard to the matter were then received.

In response to a letter sent on February 21, 1915, Mr. Swezey replied on March 26 that "no information on the rearing of the species is available in Mr. Terry's notes."

In a letter dated April 10 of the same year, however, the following notes were enclosed:

About forty-five eggs deposited in tube December 5, 1910. Chorion jet black, shining and thick, resisting dryness, 0.3 mm. by 0.15 mm., very finely parallel-striate.

One hatched December 10. The batch was placed with rotten apples and cow manure, hatching December 15. Larva long, head small, mandibles distinct and well chitinized. An adult male emerged about January 21, 1911.

Mr. Swezey, thru whose kindness the above notes are available, adds: "You see from the notes of Terry's that he did not breed *Styringomyia didyma* in its natural habitat. That is yet unknown, I guess."

The striking feature of this life history is its brevity, the entire egg, larval, and pupal stages being passed in about a month and a half. The writer knows of no other crane-flies in which this is equaled, its nearest approach presumably being in the smaller Eriopterini.

SUBFAMILY **Cylindrotominae**

The subfamily Cylindrotominae constitutes a small, isolated group of crane-flies, with twenty described species arranged in seven recent genera. All the species are Holarctic in their distribution with the exception of five species of the Oriental genera Stibadocera Enderl., Stibadocerella Brun., and Agastomyia de Meij. The group is a decadent one, having been much better developed in the early and middle Tertiaries than at present (page 764).

The adult flies are sluggish in their habits, occurring on vegetation in cool, shaded spots. The species of Cylindrotoma are brightly colored, yellow and black, but the other forms are somber in appearance and black or dark in color, the body being in some cases highly polished or metallic. The immature stages of the Cylindrotominae differ from those of all other Tipulidae, so far as is known to the writer, in being spent on various bryophytic and spermatophytic plants, on the leaves of which the larvae feed. The larvae are usually bright green in color and suggest a caterpillar in their general form. Most of them simulate their host plants to an astonishing degree. The immature stages of Cylindrotoma and Liogma are terrestrial, while those of Triogma and Phalacrocera are aquatic or nearly so.

The genera of the subfamily Cylindrotominae may be separated as follows:

Larvae

1. Body appendages very long and filiform; aquatic .... *Phalacrocera* Schin. (p. 961)
   Body appendages short, leaflike or tuberculate 2
2. Dorsal appendages all simple, on the terminal abdominal segments in a single row; terrestrial on spermatophytic plants ....*Cylindrotoma* Macq. (p. 966)
   Dorsal appendages with teeth on anterior convex side 3
3. Some of the dorsal appendages with three or four teeth on anterior face; aquatic on mosses..*Triogma* Schin. (p. 973)
   Dorsal appendages with one (*L. nodicornis*) or two (*L. glabrata*) teeth. *Liogma* O. S. (p. 969)

Pupae

1. Basal abdominal tergites without spines.......................................2
   Basal abdominal tergites with acute spines.......................................3
2. Mesonotum unarmed; segments 6 and 8 each with two powerful dorsal hooks; segment 7 with a pair of strong ventral spines; pronotal breathing horns elongate, directed backward.......................................*Phalacrocera* Schin. (p. 961)
   Mesonotum with two flattened erect lobes; segments 6, 7, and 8 naked; pronotal breathing horns small, directed slightly forward..................*Cylindrotoma* Macq. (p. 966)
3. Abdominal spines branched...........................*Liogma* (*glabrata*) (p. 969)
   Triogma (*trisulcata*) (p. 974)
   Abdominal spines not branched...........................*Liogma* (*nodicornis*) (p. 971)

The most important literature on the Cylindrotominae is as follows:

General account of subfamily. Osten Sacken, 1897; Alexander, 1914:105–106; Malloch, 1915–17 b:210–211; Lenz, 1920 b:113–115.

Phalacrocera replicata	Larva, pupa, general	De Geer, 1773; 1776:135–141, 351.
Phalacrocera replicata	Larva	Grube, 1868.
Phalacrocera replicata	Larva	Engel, 1884.
Phalacrocera replicata	General	Giard, 1895 b.
Phalacrocera replicata	Larva, general	Bengtsson, 1897. (Morphology of larva.)
Phalacrocera replicata	Larva, pupa, general	Miall and Shelford, 1897. (Morphology of larva and pupa.)
Phalacrocera replicata	Larva	Bengtsson, 1899. (Morphology of heart.)
Phalacrocera replicata	Larva	Holmgren, 1908. (Morphology of head.)
Phalacrocera replicata	Larva, pupa	Grünberg, 1910:32–35.
Phalacrocera replicata	Larva, pupa, general	Wesenberg-Lund, 1915:343–347.
Phalacrocera replicata	Larva, pupa, general	Lenz, 1920 b:127–129.
Cylindrotoma distinctissima	Larva, general	Schellenberg, 1803:22–23.
Cylindrotoma distinctissima	Larva, pupa, general	Boie, 1838:234.
Cylindrotoma distinctissima	Larva, pupa, general	Zeller, 1842.
Cylindrotoma distinctissima	General	Schiner, 1864:563.
Cylindrotoma distinctissima	Larva, pupa, general	Kaltenbach, 1874:7.
Cylindrotoma distinctissima	Larva	Wesenberg-Lund, 1915:335 (as Triogma).
Cylindrotoma distinctissima	Larva, pupa, general	Lenz, 1920 b:115–117.
Cylindrotoma splendens	Larva, pupa, general	Cameron, 1918.
Liogma glabrata	Larva, general	De Rossi, 1876.
Liogma glabrata	General	Osten Sacken, 1878 a.

Liogma glabrata.............	Larva, pupa, general...	Müggenberg, 1901.
Liogma glabrata.............	Larva, general........	De Rossi, 1902.
Liogma glabrata.............	General..............	Alexander, 1914:106–107.
Liogma glabrata.............	Larva, pupa, general...	Lenz, 1920b:117–121.
Liogma nodicornis...........	Larva, pupa, general...	Alexander, 1914:107–115.
Triogma trisulcata...........	Larva, general........	Steinmann, 1907–08.
Triogma trisulcata...........	Larva, pupa, general..	Müller, 1908–09.
Triogma trisulcata...........	Larva, general........	Wesenberg-Lund, 1915:347–348 (as *Liogma glabrata*).
Triogma trisulcata...........	Larva, pupa, general...	Lenz, 1920b:121–127.

Genus **Phalacrocera** Schiner (Gr. *bald* + *horn*)

1863 *Phalacrocera* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

Larva.— Body covered with numerous elongate, trachea-bearing filaments, the posterior pair on dorsal segments deeply forked, the others simple. Spiracular disk with dorsal pair of lobes formed by rudimentary posterior branch of branched filaments of eighth abdominal segment. Head capsule compact. Mentum with about fifteen teeth.

Pupa.— Cephalic crest low, not setiferous. Pronotal breathing horns long, almost straight. Dorsal abdominal segments with tubercles, those of sixth and eighth segments enlarged into spinous hooks; two pointed tubercles on seventh sternite.

Phalacrocera is a small genus (four species) of medium-sized to large, dull-colored flies, of which the genotype, *Phalacrocera replicata*, is European, *P. mikado* Alex. is Japanese, and the two remaining species are North American.

The adult flies of the American species are not common, the best-known, *P. tipulina* O. S., being most frequently found in or near sphagnum bogs in mountainous localities. Needham (1908a:209) found the wings of an individual of this species in the pitcher plant, *Sarracenia purpurea* Linn., in the Adirondack Mountains, together with the wings of four specimens of *Elephantomyia westwoodi* and numerous other insects. Most of the specimens that have been found by the writer were taken in close proximity to bogs.

The immature stages of *Phalacrocera replicata* have long been known, having been described by De Geer and other early workers on insect biology. More recently the life history, anatomy, and morphology have been discussed in commendable detail by several other writers (page 960). Both the larvae and the pupae are aquatic, living among submerged plants in quiet, but non-stagnant, water.

The immature stages of *P. tipulina* are very much to be desired, as the adult shows some features in its organization not found in the other species of the genus.[6]

[6] The larva of this species was discovered by J. Speed Rogers in 1920.

Bengtsson (1897) erected for this genus the group Erucaeformia, which he considered as the primitive form from which the Nematocera and the Brachycera have been derived. This group, of course, has no standing whatsoever.

Phalacrocera replicata (Linn.)

1761 *Tipula replicata* Linn. Fauna Suecica, 2d ed., p. 500–502.
1863 *Phalacrocera replicata* Schin. Wien. Ent. Monatschr., vol. 7, p. 224.

The larvae and the pupae of *Phalacrocera replicata* have been discussed in such detail by Miall and Shelford, by Bengtsson, by Holmgren, and by Wesenberg-Lund, that they are considered here only in general terms. The habits of the immature stages have been discussed by many writers since the time of De Geer. They are oftentimes rather numerous among aquatic plants such as *Ranunculus fluitans* Lam., *Fontinalis antipyretica* Linn., *Hypnum elodes* Schp., *H. exannulatum* Guenbel, and other species, feeding on these mosses and probably on other plants. These moss fragments give a green tinge to young larvae when seen thru the nearly transparent body wall. Older larvae are more opaque and are brownish green in color, indistinctly striped with pale and darker. The larva is extremely sluggish, remaining almost motionless for hours. It clings to moss stems by its large anal hooks, and, thus secured, it often sways its body from side to side as if to accelerate respiration. The larvae can go for long periods of time without fresh air. Miall and Shelford kept specimens alive for two weeks in bottles completely filled with water, and for a long time in water that had been boiled. The larvae can live for a long time out of water. Progression thru the mats of submerged vegetation is accomplished by grasping with the mandibles and the anal hooks, alternately. When alarmed the larvae curl into a rounded ball, after the manner of many caterpillars. The skin, and more especially the long body processes, are often covered with ectoparasitic organisms, such as algae and infusoria, on which small fresh-water mollusks, Planorbis, have been observed feeding and creeping about over the body of the larva. This coating of organisms, the body outgrowths, and the general coloration of the larva, give it a striking resemblance to the mosses among which it lives. De Geer (1776:355) shows that the larva can endure excessive cold. He placed four larvae in a vessel at the beginning of winter, and examined them in the following May. During the winter

the water in which the larvae lived had frozen into a solid mass, yet, on investigating the jar in the spring, De Geer found two of the larvae still alive and able to feed, and within a month both had pupated.

The larval habitat is in ponds in which a moss vegetation flourishes and in which currents keep the water in constant motion. A female fly was observed by Miall and Shelford (1897:360) depositing her eggs in the leaf axils of a submerged moss. The eggs, about sixty in number, are laid singly and adhere slightly to the moss; they are opaque, dark in color, and spindle-shaped, with the surface of the chorion irregularly pitted, and with a rosette-like micropyle at one end. Bengtsson, Müggenberg, and others believe that Phalacrocera has but a single brood in a year, the larval existence occupying about eleven months; Miall and Shelford, however, admit the possibility of a second brood. The egg stage requires from eight to twelve days and the pupal duration is seven or eight days, according to Bengtsson. According to Miall and Shelford, the pupal period is considerably longer.

During the larval development there are numerous moltings, at least eight and possibly ten; the old larval skin is cast by a simple dorsal split extending from the first to the fourth segment. Just after emerging from the egg the larva is from 2 to 2.25 millimeters in length and about 0.5 millimeter in diameter, excluding the body projections. The first larval stage (Bengtsson, 1897) lasts until the second molting. The body is provided with ten pairs of long, delicate, threadlike, lateral projections, which are located on the second to the eleventh body segments and are half as long as the body. The other projections of the older larvae are merely indicated. The attachment apparatus is placed immediately before the anus, and consists of from eight to twelve chitinized hooks, directed forward and arranged in an arcuated crossrow. The color of the body is white, almost transparent. The mouth parts show the mandibles without a prostheca and moving horizontally. The second larval stage lasts from the second until the fourth molting. The body appendages have appeared and are clearly developed, resembling in appearance and relative length those of the definitive stage. The attachment apparatus is post-anal. The body takes on a distinctly striped appearance. The mouth parts have the prostheca well developed on the mandibles, which are vertically placed and therefore have an up-and-down movement. The third larval stage represents the fully grown larva from the fourth

molt up to the time of pupation. Here the dorsum of the body is a dirty brownish green with more or less distinct brighter spots, and the venter is bright green in color. The mouth parts and the attachment apparatus are as in the second stage.

The pupa is comparatively active, moving about by flexion of the abdomen. Its usual position is vertical, with the tips of the breathing horns just reaching the surface of the water. This vertical position the pupa maintains by grasping the vegetation with its caudal abdominal hooks. At times the pupa descends beneath the water by clinging to the vegetation, but a submergence of six hours causes asphyxiation. The pupal existence was determined by Miall and Shelford as eleven days. When the adult emerges, the cast pupal skin is left attached to a moss leaf by the dorsal abdominal projections at the posterior end of the body.

Larva.— Length, about 25 mm.

Young larvae distinctly greenish, especially on ventral side, this coloration caused, at least in part, by contents of alimentary canal showing thru body wall; older larvae more opaque, brownish green in color; dorsum with an indistinct striping of brown and whitish; ventral surface whitish.

Head entirely retractile within prothorax and usually so retracted except when larva is feeding; opening transverse. Prothorax, viewed from above, roughly rounded, anterior margin convex; on ventral surface traversed by a weak suture. Meso- and metathorax narrow. Abdominal segment 1 indistinctly divided into two annuli, the more basal one very narrow; abdominal segments 2 to 7 divided into a narrow basal ring and a much broader posterior ring, each of these annuli still further subdivided into two annulets. Body provided with numerous elongate trachea-bearing filaments, both simple and branched, giving larva a very bristly appearance (Plate LXXXIII, 448), these spines arranged as follows: *tergites* with both simple and bifurcated filaments; on posterior part of pronotum two short, simple filaments; on meso- and metanotum, two pairs of simple filaments; on abdominal segment 1, an anterior pair of simple, and a posterior pair of deeply branched, filaments; segments 2 to 7 with basal ring unarmed, posterior ring with an anterior pair of simple, and a caudal pair of deeply branched, filaments; segment 8 with only a branched pair, anterior branch long, slender, posterior branch very small, its outer face heavily chitinized and forming dorsal lobes of spiracular disk; *pleurites* with all the filaments simple; one on posterior part of prothorax, and on anterior part of each of the other two thoracic segments; posterior filament on these latter nearly vestigial; two unequal filaments on first abdominal segment; segments 2 to 7 with one filament on basal ring and two on posterior ring, the anterior one the longest; segment 8 with a single rudimentary filament; *sternites* with all the filaments simple; prosternum without filaments; meso- and metasternum with a strong filament near lateral margins; abdominal segment 1 with two pairs of filaments, posterior pair the longer and more widely separated; segment 2 with three pairs of filaments, anterior pair very short; segments 3 to 7 with four pairs of filaments and an additional median one, arranged as follows:

two pairs of small filaments on basal ring, the anterior pair more widely separated, two pairs of much longer filaments on posterior ring, the last pair more widely separated, longer, and tipped with blackish, between them a tiny median filament. Chaetotaxy as follows: tergites with four solitary setae along anterior margin of prothorax, and two setae just laterad of each dorsal filament of prothorax and posterior filaments of meso- and metathorax; abdominal segments with a seta laterad of each simple and branched filament; pleurites with a stiff seta at base, and out toward apices, of middle lateral filaments; sternites with a group of about four stiff setae on either side of posterior ring of prosternum, and a single stiff seta on either side of median line; meso- and metasternum with a lateral group of setae; a seta laterad, and another at about midlength, of each of the posterior pair of ventral filaments.

Spiracular disk with ventral lobes elongate, slightly recurved, the posterior face intensely blackened, chitinized, each lobe with two acute spines at tip, with two setae near them; a stiff seta on side of base of each ventral lobe; dorsal lobes as already described, the rudimentary posterior branch of last furcate dorsal filament much smaller than in ventral lobes, the posterior face heavily blackened; spiracular disk rhombic in form, white, and having almost the appearance of porcelain. Spiracles situated between bases of dorsal lobes. Skin about spiracles capable of retraction so as to form a deep recess.

Head capsule rather short, almost conical, formed of two large lateral plates and a somewhat smaller and shorter prefrontal plate. Mentum with an outer (ectolabial) part and an inner (endolabial) part; mentum a triangular or somewhat pentagonal plate, strongly chitinized, fore margin with about fifteen teeth; mandibles working against teeth of both endo- and ectolabia. Antenna of a single segment, bearing on its truncated apical end a few sensory papillae. Mandibles small but strong, curved inward at tip and furnished with a fringe of setae, which assist in closing the mouth opening. Maxilla expanded into flattened, shovel-like structures, inserted high on side of head; palpus with a number of sensory papillae at apex, and with a porous plate on outer side which seems to be an organ of hearing.

Pupa.— Length, 16–18 mm. (Miall gives length up to 20 mm.)
Width, d.-s., 2.9–3.3 mm.
Depth, d.-v., 2.7–2.9 mm.

Coloration greenish brown, in alcohol a paler yellowish brown; a very broad dorso-median dark brown stripe which is narrowly margined laterally with yellowish; dorsum of abdomen suffused sublaterally with dusky, extreme lateral margins of body yellowish; ventral surface with two broader sublateral stripes and a very narrow ventro-median stripe.

Anterior end of body very deep and thick, as is usual in this group of crane-flies. Abdomen greatly depressed, with lateral margins very thin and flattened. Cephalic crest low, nonsetiferous, located between antennal bases. Labrum broad basally, narrowed toward apex, which is broadly rounded; two setae at base of labrum. Labial lobes subcircular in outline. Maxillary palpi elongate, bent strongly backward so as to lie along flattened cheek. Antenna rather elongated, extending far beyond origin of wing pad (Plate LXXXIII, 449). Thorax very deep, flattened above. Pronotal breathing horns, which are broken in the writer's specimens, seen from other descriptions to be rather elongate, almost straight, and slightly divergent; two small setae between bases of breathing horns; two groups of setae on anterior part of pronotum before breathing horns. Mesonotum (Plate LXXXIII, 449) with six

small, setiferous tubercles, one above each wing axil, the other four arranged in a trapezoid on dorsum with the anterior pair closer together; metanotum with six setiferous tubercles, four of which are median in position, the other pair at antero-lateral margin, near base of halteres. Wing sheaths ending about opposite apex of second abdominal segment. Leg sheaths ending before apex of third abdominal segment.

First abdominal segment similar to metanotum; segments 2 to 7 indistinctly subdivided into a narrow basal ring and a much broader posterior ring; basal ring unarmed except for a seta on pleural margin and a trapezoid of tubercles on sternum; posterior annulus armed as follows: tergites with four tubercles arranged in a quadrangle and located in the dark median stripe, posterior tubercles with a stiff seta just laterad of each; a lateral seta on a line with anterior tubercles; two lateral setae on a level with posterior tubercles, the proximal one considerably the larger; these setae located in the yellow sublateral stripe; pleural margin with two setiferous tubercles with an acute subappressed spine between them; a seta immediately ventrad of anterior tubercle; on segments 6 and 7, spine closer to caudal margin of segment, and tubercle beyond it lacking; sternites with a trapezoid of naked tubercles on basal ring, posterior pair the closer together; a trapezoid of larger setiferous tubercles on posterior ring, anterior pair the closer together; posterior punctures each having two setae, with an additional slender seta laterad of these in the lateral dark stripe; dorsum of segment 6 (Plate LXXXIII, 450) with posterior pair of tubercles replaced by two powerful lobes directed caudad and laterad; segment 7 unarmed on dorsum, sternum with two acute spines near caudal margin; segment 8 with lateral angles produced dorsad into slender lobes which are spinous on all the faces; caudal angles directed caudad into slender lobes, acute at tips and with anterior inner face spinous and bearing a few setae. Male cauda with sternal valves very blunt and rounded, on either side of ventro-median line produced caudad into an acute spine. Female cauda with dorsal acidothecae a little longer than the more slender sternal valves, both pairs much exceeded by caudal angles of eighth segment.

Nepionotype.— Larva, Denmark.
Neanotype.— Pupa, Denmark.
Paratypes.— One larva and one pupa.

(The writer is indebted to Dr. C. Wesenberg-Lund for this material, as well as for several other interesting European crane-fly life histories.)

Genus **Cylindrotoma** Macquart (Gr. *cylinder* + *I cut*)

1834 *Cylindrotoma* Macq. Suit. à Buff., vol. 1, Hist. Nat. Ins., Dipt., p. 107.

Larva.— Body covered with simple tubercles, a median dorsal row and a double ventral row. Spiracular disk large, surrounded by small lobes. Head capsule compact. Mentum with about fifteen teeth.

Pupa.— Pronotal breathing horns short, cylindrical, directed strongly ventrad. Mesonotum with two flattened lobes directed cephalad. Abdomen unarmed with spines or lobes.

Cylindrotoma is a small genus including six species distributed thruout the North Temperate Zone, three of these species occurring in North America.

The adult flies of *Cylindrotoma tarsalis* Johns., the only species that the writer has ever found in nature, are common on rank vegetation in cool, boggy, and swampy woods. The immature stages of the genotype, *C. distinctissima* (Meig.), have long been known, having been discussed by Schellenberg (1803), Boie (1838), Zeller (1842), Kaltenbach (1874), and others. The larva shows some resemblance to that of Phalacrocera, but is almost entirely terrestrial in its habits, feeding on the leaves of various spermatophytic plants such as *Caltha palustris, Anemone nemorosa, Ranunculus repens*, Chrysosplenium, *Stellaria nemorum, Sanicula europaea, Viola biflora, Valeriana officinalis*, Allium, and others. It attains a length of nearly 25 millimeters, and is narrow, depressed, tapering to either end, and of a grass-green color. There is a slight dorsal ridge from which a row of short, fleshy spines projects, these spines being directed backward and one spine on each segment being longer than the others. There is a broad lateral margin bearing very short processes, and there are also eight pairs of ventral ridges without hooks and a pair of longer backward-directed processes near the anus. The pupa affixes itself to stalks or leaves by the caudal end, to which the remains of the last larval skin adhere. The larvae generally remain on the lower surface of the leaves, on which they feed, gnawing holes in them. When about to pupate they generally leave their food plants and fasten themselves on grass blades and leaves near by, usually pupating the following day. From the foregoing observations it would seem that there are in the various localities two generations a year, one in the spring and the other in the autumn.

The life history of *C. splendens* has recently been worked out in considerable detail by Dr. A. E. Cameron, thru whose kindness the writer has received specimens for study.

Cylindrotoma splendens Doane

1900 *Cylindrotoma splendens* Doane. Journ. N. Y. Ent. Soc., vol. 8, p. 197.
1900 *Cylindrotoma juncta* Coq. Proc. Wash. Acad. Sci., vol. 2, p. 401.
1918 *Cylindrotoma splendens* Cameron. Ann. Ent. Soc. Amer., vol. 11, p. 67–89.

Cylindrotoma splendens is an interesting crane-fly occurring from British Columbia northward to Alaska. Dr. Cameron's excellent notes on the life history of this species are abstracted in detail on pages 708 to 710 of this paper. The following descriptions were made from material sent

to the writer by Dr. Cameron, a few details being added from Dr. Cameron's published notes.

Larva.— Length, 15–17 mm.
Width, d.-s., 2.4–2.5 mm.
Depth, d.-v., 1.5 mm.

Coloration light chlorophyll green, with two narrow, pale brown lines on dorsum, extending from posterior end, above spiracles, anteriorly, becoming more expanded and diffused on fore part of body.

Body very depressed, both dorsal and ventral surfaces being flattened, lateral margins sharp (Plate LXXXIV, 453). Head completely retractile within prothorax. Skin delicately reticulated and roughened. Thorax, viewed from above, semicircular in outline, margined with about four tubercles on either side, anterior pair the largest, separated by a V-shaped notch. Pronotum with an anterior pair of small tubercles and a larger median tubercle behind, directed backward; segments 2 and 3 each with lateral margins two-toothed, the anterior tooth the larger and more pointed; a blunt dorsal tubercle on anterior margin and a larger one behind. Abdominal segments indistinctly divided into four annuli which are poorly delimited; the two basal annuli narrow and corresponding to basal annulus of most crane-fly larvae, the third annulus the largest and bearing a slender lateral tooth; other segments less distinctly divided serrately on lateral margin; dorsum of abdominal segments with a row of blunt median tubercles, there being four on each segment, the first very small to vestigial, the third slender, the last the stoutest; on venter of abdominal segments 1 to 7, near posterior margin, a fleshy conical lobe (pseudopodium) on either side of median line, these being smaller on anterior segments (1 to 4), and much larger and paler on posterior segments (5 to 7). Spiracular disk very large and flattened, obliquely truncated, surrounded by six small lobes, the dorso-lateral pair small, widely separated, the ventro-lateral pair much larger, the ventral pair very small, slender. Spiracles very small, circular, widely separated, the distance between them about equal to six times diameter of one.

Mouth parts with labrum linguliform, terminating in four teeth, external pair smaller than internal pair. Mentum with seven teeth on either side of small median one, the first and the third on either side being the largest. Hypopharynx with two rows of small teeth. Antenna two-segmented; basal segment elongate, pyriform; apical segment thimble-shaped. Mandible (Plate LXXXIV, 454) powerful; cutting edge with about five marginal teeth and two dorsal teeth; a large basal prostheca. Maxilla large; outer lobe fringed with stiff hairs; a few acute sensory bristles situated on elevated papillae, two on cardo, one on outer lobe of maxilla; maxillary palpi short, cylindrical, apex obliquely truncated and provided with numerous sensory knobs, on side near tip a circular porous plate (which as it appears in Phalacrocera is suggested by Bengtsson as probably being an organ of hearing).

Pupa.— Length, 11.7–14 mm.
Width, d.-s., 2–2.8 mm.
Depth, d.-v., 1.4–2 mm.

Color of live pupa, leaf green; preserved specimens much paler, yellowish; pronotal breathing horns grayish white; margins of abdomen nearly translucent.

Labrum narrow, apex evenly rounded. Labial lobes stout, separated by labrum, at tip narrowed and somewhat pointed. Maxillary palpi long and stout, just beyond base bent strongly backward. Antennae rather short, bases not widely separated (Plate LXXXIV, 456). Thorax very deep, much flattened anteriorly (Plate LXXXIV, 455). Pronotal breathing horns short, cylindrical, slightly divergent, apex of each a little expanded. Mesonotum at declivity with two flattened plates, which are blunt and directed cephalad and slightly laterad; above wing axil a smaller tubercle. Wing sheaths ending just before apex of second abdominal segment. Leg sheaths ending just before apex of third abdominal segment; tarsi ending about on a level.

Abdomen strongly depressed, lateral margins carinate; segments distinct, unarmed, subdivided into a narrow basal ring and a much broader posterior ring; segments 2 to 5 a little longer than segments 6 and 7. Male cauda with valves divided into two rounded lobes by a small median notch. Female cauda with dorsal valves straight, a little longer and much stouter than the slender sternal valves.

Nepionotype.— Westholme, Vancouver Island, B. C., May 15, 1917.
Neanotype.— Female pupa with type larva.

Genus **Liogma** Osten Sacken (Gr. *smooth* + *furrow*)

1869 *Liogma* O. S. Mon. Dipt. N. Amer., part 4, p. 298.

Larva.— Body covered with elongate, leaflike projections, dorsal ones with one or two teeth on anterior convex face. Spiracular disk surrounded by four lobes. Head capsule compact. Mentum with about fourteen teeth.

Pupa.— Metanotum and abdominal tergites with elongate spines, branched in *L. glabrata*, simple in *L. nodicornis*.

The genus Liogma includes three known species, of which the genotype, *Liogma nodicornis* (O. S.), is American. The adult flies of this species are sluggish, and are found resting on vegetation growing in and about shaded ponds and similar situations.

In Europe the life history of *L. glabrata* (Meig.) has been worked out by De Rossi (1876), by Wesenberg-Lund (1915:347–348), and in considerable detail by Müggenberg (1901). The larvae were found in the woods near Berlin, in wet, grassy spots where the moss *Hypnum squarrosum* Brch. & Schp. occurs. The complete metamorphosis of the insect takes one year, the larval life requiring the greater part of this period. The egg stage lasts from eight to ten days and the pupal stage from eleven to twelve days. The duration of adult life is not known, but it is certainly short, occupying but a few weeks at the most.

Near Berlin the flies emerge during the first half of July. The males appear first, the females later, and the latter are always seized in copulation

by the males just after they have forsaken the pupal skin and while still teneral and undeveloped. Each female lays about sixty eggs, and these are deposited singly on the leaves or branches, or attached lightly to the axils of the leaves, of *Hypnum squarrosum*. Egg deposition begins from one-half to one day after copulation, and may be extended, with many interruptions of greater or less extent, thru a whole day. The eggs are from 1 to 1.2 millimeters long, spindle-shaped, yellowish green in color, the chorion with a reticulate sculpturing. After the accomplishment of oviposition the exhausted female soon dies. The larvae when first hatched are 2 millimeters in length and do not yet possess the beautiful moss-green color of the later stage. With the exception of the chitinized head capsule, they appear ashy gray. The numerous thornlike projections are to be noted already in the same positions as those of the developed larva, but do not show the branching of the later stages. In the autumn the young larva grows very slowly, and during the winter it is still very small and difficult to detect. In the spring the growth is greatly accelerated, and the larva becomes fully grown during the latter half of June. While attaining its growth the larva molts several times, probably at least eight — the number determined for Phalacrocera by Bengtsson. Pupation occurs in the moss where the larva happens to be. In its green color, with brown blotches, the larva remarkably simulates its host plant and the effect of the shadows cast by the plant stems and leaves. The larvae are extremely sluggish in their habits.

The American species *Liogma nodicornis* has been found in various mosses of the genus Hypnum (Alexander, 1914). The immature stages of this species are discussed below.

The following keys separate the species of Liogma:

Larvae

Prothoracic segment bearing four conspicuous dorsal projections about on a line; meso- and metathorax with two pairs of dorsal appendages, each bearing two lateral teeth in front; second abdominal segment with four dorsal appendages, the last two bearing two teeth in front (Palaearctic) . . . . *glabrata* (Meig.) (p. 969)

Prothoracic segment bearing four inconspicuous dorsal tubercles; meso- and metathorax with two pairs of dorsal appendages, the anterior pair small, both pairs simple; second abdominal segment with four dorsal appendages, the last two bearing a single small tooth in front (Nearctic) . . . . *nodicornis* (O. S.) (p. 971)

Pupae

Pronotal breathing horns directed cephalad and dorsad; mesonotum bearing two pairs of spines, the more anterior being the smaller, situated just behind breathing horns, posterior pair the larger; metanotum with two pairs of spines; abdomen with first tergite bearing two pairs of spines, the first having two lateral branches, the second simple; second tergite bearing two pairs of spines, the first with two lateral branches, the second with one branch; third tergite bearing three pairs of spines, the first very short and simple, the second with two lateral branches, the third with one branch; tergites 4 and 5 with three pairs of branches, the first two similar to those of third segment, the last possessing two lateral branches.. *glabrata* (Meig) (p. 969)

Pronotal breathing horns directed cephalad and ventrad; mesonotum spineless; metanotum with one pair of spines; abdominal tergites bearing but a single pair of appendages, which are unbranched and correspond in position to the last or more posterior of those of the European species.................................... *nodicornis* (O. S.) (p. 971)

Liogma nodicornis (O. S.)

1865 *Triogma nodicornis* O. S. Proc. Ent. Soc. Phila., vol. 4, p. 239.
1869 *Cylindrotoma nodicornis* O. S. Mon. Dipt. N. Amer., part 4, p. 301.
1887 *Liogma nodicornis* O. S. Berl. Ent. Ztschr., vol. 31, p. 226.

Liogma nodicornis, the only American species of the genus, is widely distributed thruout the Northeastern States. The larvae are found in moss — *Hypnum cupressiforme* Linn. and related species. They are the most sluggish of any crane-flies known to the writer, moving only with great slowness and much of the time appearing to be quite dead. They crawl about among the stems of their host plant and probably never leave it, even to pupate. The pupal duration indoors is not more than six days. Further details of the life history are given by the writer in an earlier paper (Alexander, 1914).

Larva.— Length, 14.5–15 mm.
Width, 3 mm.
Depth, 2.5 mm.

Color of live larva light green, the numerous spines covering the body darker; sides with seven black marks, the first on first abdominal segment, the last on seventh abdominal segment; the marks on ends the smallest and least distinct, the five intermediate marks large and conspicuous; these marks all lying parallel to one another; posterior face of ventral lobes surrounding stigmal field intensely black.

Prothorax in front (Plate LXXXV, 462) sloping from anterior end, on ventral slope provided with liplike lobes, with a transverse slit from which head capsule is exserted; upper lip the higher, not strongly chitinized, provided with a few small, scattered bristles, these more numerous on sides of lobe; lower lip not so high, with small, scattered bristles not arranged in a row as in *L. glabrata*; at angle of slit a small rounded lobe bearing a small bristle. Dorsal body appendages reduced to a pair of lobes in front, separated by a space a little greater than diameter of one, and a pair of smaller lobes behind, very widely separated; lateral body appendages long, conspicuous; ventral body appendages not apparent. Meso- and metathorax swollen and arched ventrally like prothorax; dorsal appendages two, a small conical

one in front and a much larger one behind bearing a small tooth in front and with its tip directed backward; lateral appendages, viewed from above, two in number, anterior one the larger, directed sharply backward, the second smaller, conical; ventral appendages, viewed from side, four, anterior pair the larger, posterior pair small, slightly behind the others.

Dorsal appendages of abdominal segments (Plate LXXXV, 457) as follows: first segment with two pairs of appendages; anterior pair the shorter, conical, tips strongly recurved and bearing a tiny tooth on anterior face at about midlength; posterior pair much longer, with tips bent strongly backward, a small tooth on anterior face at about one-third length from base; segments 2 to 7 with four pairs of appendages, the first pair very small, conical, the second exactly similar but larger, the third and fourth pairs similar to appendages of first abdominal segment; the tiny anterior appendage largest on second segment, gradually becoming smaller toward end of body. Lateral abdominal appendages as follows: first segment with three pairs of appendages, the first directed laterad, the posterior two more recurved and directed caudad; segments 2 to 7 with four pairs of appendages, the first very small, situated at antero-lateral angle of segment, the other three subequal and directed caudad. Ventral abdominal appendages as follows: first segment with three pairs of appendages, which are successively larger from the short anterior one to the large posterior one; segments 2 to 7 with five pairs of appendages, the first three small, the fourth intermediate in size between them and the enlarged fifth pair. Eighth segment bearing spiracular disk and its lobes; dorsal side of field with a pair of long, slender lobes bent conspicuously cephalad. Spiracular disk (Plate LXXXV, 461) small, oval, the two rounded-oval spiracles situated side by side and close to each other, inclined toward each other and capable of being closely appressed; ventral lobes of disk directed ventrad, inner faces of lobes with a conspicuous jet-black line, tip of each lobe ending in a sharp recurved hook. (Müggenberg regards these lobes as representing the ninth abdominal segment.) Ventral surface of terminal segments with small protuberances.

Head completely retractile into first thoracic segment. Mentum (Plate LXXXV, 458) with about seven teeth on either side, terminal pair the larger, separated by a V-shaped notch. Antenna (Plate LXXXV, 460) two-segmented, basal segment elongate-cylindrical, tip very short, thimble-shaped, with a diameter less than that of elongate basal segment. Mandible (Plate LXXXV, 459 and 460) many-toothed on inner face, with a prominent basal prostheca; mandibles working vertically against teeth of mentum. Maxilla (Plate LXXXV, 458) with palpi very short, broad, basal segment chitinized, tip narrow, pale.

Pupa.— Length: male, 10.4–11.4 mm.; female, 10–13 mm.
Width, d.-s.; male, 2–2.2 mm.; female, 2.2–2.6 mm.
Depth, d.-v ; male, 1.9–2.2 mm.; female, 2.1–2.5 mm.

Living pupae with pronotal breathing horns light yellow, the terminal half a little more brownish; a brownish black mark on prescutum; abdomen greenish, more yellow behind; dorsal spines clear light green thruout or with tips in some specimens a little infuscated. (In pupae preserved in alcohol, the greenish colors are lost, the dark brownish black mark of the mesonotal prescutum is irregularly U-shaped, with the arms of the U directed backward, and the dark color is produced caudad and cephalad along the dorso-median line; there is a triangular or rounded black spot on either side of the scutellar lobe; on the metanotum is a large blackish median blotch, which is continued cephalad onto the mesonotal postnotum; the abdomen has an interrupted brownish black longitudinal line along either side of the midline of the dorsum; the posterior margin of each tergite is suffused with

brown.) In old and fully colored pupae, bases of dorsal spines brown, with the tips paler; head and thorax with appendages brown, in some specimens very dark; abdomen yellowish.

Cephalic part of head very flat and broad, without spines but with a small, blunt tubercle between antennal bases. Labrum transversely wrinkled, narrowed to the bluntly rounded apex. Labial lobes large, divergent, each lobe rectangular with angles rounded. Sheaths of maxillary palpi rather long, curved strongly backward. Antennal sheaths rather enlarged, directed cephalad, bending around anterior margin of eye and thence directed caudad, ending just beyond knee joint of fore legs. (In older pupae, the peculiar nodose antennal segments of the adult show thru the sheath.) Pronotal breathing horns (Plate LXXXV, 464) large, conspicuous, directed dorsad and laterad, the terminal half bent rather suddenly cephalad. Mesonotum transversely wrinkled. Metanotum (Plate LXXXV, 463) with two long, slender spines, arising beyond midlength of segment, directed caudad and slightly dorsad. Wing sheaths broad, reaching posterior margin of second abdominal segment. Leg sheath ending just before posterior margin of third abdominal segment; fore legs the shortest, hind legs the longest.

Abdominal segments with a narrow basal ring and a broader posterior ring; segment 1 about half as long as segment 2; tergites 1 to 7 with a pair of long, slender, spinous projections, shortest on anterior segment, longest on seventh segment, these projections arising from near caudal margin of segment, directed dorsad and caudad, those of anterior segment almost parallel, those of posterior segments more divergent; segments 2 to 7 having lateral margins produced into three sharp spines, one on basal ring and two on posterior ring of each segment, these spines directed laterad and caudad, the terminal spines more sharply caudad than the other two; abdominal sternites armed as follows: segment 3 with a small, subapical spine on either side, these spines very widely separated, segment 4 with similar spines but larger and more prominent, segments 5 to 7 similarly armed but with another pair of small spines about midlength of segment and much nearer midline of body, segments 2 to 7 with a subbasal triangular pit on either side, these pits widely separated; eighth tergite with caudal margin rounded, concave, the lateral angles produced backward, upward, and slightly outward as strong spines; suture on ventral surface incomplete; two small spines on either side of middle line of body; posterior margin of segment produced caudad as two strong spinous projections. Male cauda with sternal valves rather long, tipped with two to four acute spines, in some specimens with two spines on one of the lobes and only one on the other; tergal valves a little rounded at tips, slightly longer than sternal valves. Female cauda (Plate LXXXV, 465 and 466) with sternal valves slender, feebly notched at tips; tergal valves broader, rounded at tips, and with a deep median split.

Nepionotype.— Coy Glen, Ithaca, New York, May 8, 1913.
Neanotype.— Ithaca, May 30, 1913.
Paratypes.— Larvae and pupae with types; others from Orono, Maine, June 17 and 19, 1913.

Genus **Triogma** Schiner (Gr. *three + furrow*)

1863 *Triogma* Schin. Wien. Ent. Monatschr., vol. 7, p. 223.

Larva.— Body covered with elongate leaflike projections, some of the dorsal ones with as many as four teeth on anterior convex face. Spiracular disk surrounded by four lobes.

Pupa.— Dorsum of abdomen with elongate branched spines.

The genus Triogma includes but three known species, the genotype *Triogma trisulcata* (Schum.) of Europe, *T. kuwanai* (Alex.) of Japan, and *T. exculpta* O. S. of the eastern United States. The last-named species is very rare and its habits are entirely unknown.

The first reference to the immature stages of *T. trisulcata* is by Steinmann (1907–08), who discusses the larva as that of an unknown species of Phalacrocera. The true identity of this insect was made known by Müller (1908–09). Steinmann found the larvae at Säckingen at the end of April, fourteen days after the melting of the snow. They were found in mountain streams, attached to and living among the stems of the aquatic moss *Fontinalis antipyretica* Linn., to which they clung firmly by means of two strong chitinized hooks at the caudal end of the body. The larva resembles to a startling degree the moss on which it lives. Along the dorsal surface are two rows of leaflike appendages, each of the abdominal segments having three such appendages, of which the most anterior one is the shortest and the posterior one is the longest. The anterior appendage is untoothed, the others have as many as four teeth on the anterior face. The pleural region likewise bears a row of leaflike structures, while the ventral surface shows a double row of small, knoblike leaflets. Thru the strong accentuation of the dorsal and the two lateral rows, there is produced a copy of the ternate condition of the leaf arrangement in Fontinalis.

The larva of *T. trisulcata* (Plate LXXXIII, 452) is of a light green color marked with darker blotches, and measures 19 millimeters in length. The longest body appendage is 1.5 millimeters in length. Müller found larvae and also pupae. The pupa is characterized by the possession of somewhat similar appendages to those of the larva, the dorsal row showing the peculiar branched condition found in the larva.

SUBFAMILY **Tipulinae**

The subfamily Tipulinae comprises a remarkably homogeneous assemblage of usually large species. It is made up of a relatively few but in some cases very extensive genera, which are found thruout the world. Efforts have been made in the past to maintain three tribes — the Dolichopezini, the Ctenophorini, and the Tipulini. It has become increasingly difficult, however, to define these groups on the constant accession of exotic genera and species. A study of the immature stages likewise

fails to substantiate the validity of these groups, and, for the present at least, or until other and better characters may be found, it is better to eliminate the Dolichopezini and the Ctenophorini, founded, as they are, on insufficient or sexual characters.

The species of the Tipulinae include the largest crane-flies known, some exotic species of Ctenacroscelis attaining a wing expanse of nearly 10 centimeters. In North America the largest species are representatives of the genera Longurio and Holorusia. The great majority of the species in this subfamily are well above the average in size, this feature alone being sufficient to eliminate all but a very few of the other groups of Tipulidae. The smallest member of the subfamily Tipulinae known to the writer is *Microtipula amazonica* Alex., of Brazil, in which the wing of the male measures but 7.2 millimeters in length and is very long and narrow. Practically all of the common local species of this group belong to the two genera Tipula and Nephrotoma.

The immature stages of members of the subfamily Tipulidae are found in a wide range of habitats. Some species of Tipula are almost entirely aquatic in the larval state. The majority of the known species live in moist earth near water, or beneath damp cushions of moss. Some, such as Oropeza, live in much drier mosses on exposed rocks. A rather considerable number of species (Brachypremna, Ctenophora, Dictenidia, and several species of Tipula) live in decaying wood or beneath the bark of prostrate trunks. Tanyptera lives in wood which is relatively sound, and this represents the extreme development of this tendency in the family.

The larvae are never very slender, and are usually very plump and terete. In a few cases only is the body decidedly depressed. There is a definite arrangement of setae on the body, there being none on the anterior annulus of the abdominal segments except a single seta on the pleura of either side. The spiracular disk is surrounded by six lobes, a number not found in the Limnobiinae. In Dolichopeza the number is described as being five, the normal number in the Eriopterini, but all other features of the genus are essentially tipuline. In a few species the number of lobes is increased to eight. In the genus Tanyptera the lobes are exceedingly reduced in size so that the caudal end appears almost naked and exposed. The spiracles are always present and in some cases are very large. The anal gills are almost always present and are variously

developed according to the habitat. The head capsule is remarkably uniform thruout the group, being broad, compact, and massive, with the posterior incisions shallow and the prefrontal sclerite very large and usually distinct. The labrum is usually conspicuous, transverse, with fringes of hairs. The mentum has from seven to nine teeth along the anterior margin, and is deeply split behind but not completely divided. The hypopharynx consists of a narrow, flattened plate, with the basal lateral angles produced into strong arms and the anterior margin having usually five teeth, the teeth being rarely more numerous and in some cases obsolete. The antennae are cylindrical, and are stoutest in the wood-inhabiting species; in many species of Tipula and Prionocera they are long and slender, the length being about four times the diameter; the apical papilla, in some cases obsolete, is usually very small and is flattened. The mandibles are not large in proportion to the size of the capsule; they have few teeth, in some species only a dorsal and a ventral tooth in addition to the apical point; the prosthecal appendage is variously developed. The maxillae are simple and generalized in structure.

The pupae are fairly uniform in structure thruout the subfamily. The tips of the sheaths of the maxillary palpi are strongly curved, or, in the majority of species, actually recurved. The pronotal breathing horns are variously formed, but in practically all species they are short, cylindrical, and with the tips but little expanded. In some genera (Longurio, Prionocera, and Tipulodina) the breathing horns are greatly elongated, and, in some cases at least, are slightly unequal in length, the longer measuring nearly half the length of the body. In some genera, such as Prionocera and Holorusia, the horns are split at their tips into two divergent flaps. The only short, clavate horns in the subfamily are those of the genus Tanyptera. The mesonotum is often provided with four or six variously developed tubercles. The abdominal segments are almost always armed with transverse posterior rows of spines, these ranging in number from about four to twenty.

The large size of the larvae and the pupae will, as a rule, easily separate this subfamily from almost all members of the Limnobiinae. The few large members of the latter group are readily separated by the characters outlined above.

The following keys separate the genera of the subfamily Tipulinae:

Larvae

1. Spiracular disk surrounded by five lobes; living in moss....... *Dolichopeza* Curt. (p. 981)
   Spiracular disk surrounded by four or six lobes, or with lobes indistinct.............. 2
2. Spiracular disk with lobes indistinct; living in nearly solid or semi-decayed wood. *Tanyptera* Latr. (p. 988)
   Spiracular disk with lobes distinct.. 3
3. Spiracular disk with four slender, hornlike lobes.......... *Tipula* (*selene* Meig.) (p. 1016)
   Spiracular disk with six lobes.. 4
4. Anal gills pinnately branched............................. *Longurio* Loew (p. 990)
   Aeshnasoma Johns. (p. 993)
   Anal gills not pinnately branched.. 5
5. Antepenultimate segment of abdomen with a strong lateral tubercle. *Oropeza* Needm. (p. 982)
   Antepenultimate segment of abdomen without such a tubercle...................... 6
6. Dorsum of head behind antenna with a slender, flexible spine; living in wood. *Ctenophora* (*apicata* O. S.) (p. 986)
   Dorsum of head without such a spine... 7
7. Lobes surrounding spiracular disk elongate, digitiform, fringed with long hairs. *Prionocera* Loew (p. 995)
   Lobes surrounding spiracular disk less elongate.................................. 8
8. Size large (over 50 mm.); spiracular disk with the six moderately long lobes fringed with long hairs; mandible small, with a dorsal and a ventral tooth; found in western North America.. *Holorusia* Loew (p. 993)
   Size smaller; if large (*T. abdominalis*), the lobes surrounding disk bifid; mandible with two or three ventral teeth................................ *Tipula* Linn. (p. 998)
   Nephrotoma Meig. (p. 1016)

Pupae

1. Pronotal breathing horns very long, slender, the longest one nearly if not quite half length of body.. 2
   Pronotal breathing horns short, cylindrical or flattened, subequal in size............. 3
2. Length 40 mm.; longest breathing horn 18 mm.; maxillary palpi not recurved at tips; venation with petiole of cell M_1 very short.................. *Longurio* Loew (p. 990)
   Length 20 mm.; longest breathing horn 9 to 10 mm.; maxillary palpi recurved at tips; venation with petiole of cell M_1 longer.................... *Prionocera* Loew (p. 995)
3. Pronotal breathing horns short, compressed, deeply bicrenulated; living in wood. *Tanyptera* Latr. (p. 998)
   Pronotal breathing horns cylindrical... 4
4. Maxillary palpi not recurved at tips.. 5
   Maxillary palpi recurved at tips... 6
5. Pronotal breathing horns with apices deeply split; mesonotum with two tubercles; abdominal segments with fourteen to thirty-four spines; found in Western States; living in mud.. *Holorusia* Loew (p. 993)
   Pronotal breathing horns short, slender, apices not split; mesonotum with eight tubercles; abdominal segments with four powerful spines near posterior margin; found in Southern States; living in wood............................ *Brachypremna* O. S. (p. 984)
6. Mesonotum with two spines; ventral abdominal spines six to eight; fore and middle tarsi subequal, shorter than hind tarsi; living in wood.......... *Ctenophora* Meig. (p. 986)
   Characters not as above.. 7
7. Mesonotum with a large, roughly triangular, reticulated area on either side of median line; dorsum of cauda with four lobes...................... *Oropeza* Needm. (p. 982)
   Mesonotum unarmed or with four or six lobes; dorsum of cauda with six, or rarely four, lobes.. *Tipula* Linn. (p. 998)
   Nephrotoma Meig. (p. 1016)

The most important literature on the Tipulinae is as follows:

Dolichopeza albipes	Pupa	Beling, 1879:44–45 (as *sylvicola*).
Dolichopeza albipes	Larva, pupa, general	Beling, 1886:189–191 (as *sylvicola*).
Tanyptera atrata	General	Perris, 1840:92; 1849:333.
Tanyptera atrata	General	Nördlinger, 1848.
Tanyptera atrata	General	De Rossi, 1882.
Tanyptera atrata	Larva, pupa, general	Gercke, 1884, Pl. I, figs. 12–19.
Tanyptera atrata	General	Hermann, 1880.
Tanyptera atrata ruficornis	Larva	Gerbig, 1913:156–158 (as *Ctenophora flavicornis*).
Tanyptera fumipennis	Larva, pupa, general	Malloch,1915–17 b:194–195; 1919.
Dictenidia bimaculata	Larva	Bouché, 1834:32.
Dictenidia bimaculata	General	Zetterstedt, 1851:4023.
Dictenidia bimaculata	Larva, pupa, general	Weyenbergh, 1872.
Dictenidia bimaculata	General	Beling, 1873 b:575.
Dictenidia bimaculata	General	Czizek, 1913:102.
Ctenophora flaveolata	Larva, pupa, general	Réaumur, 1740, Pl. I, fig. 9.
Ctenophora flaveolata	General	Zetterstedt, 1851:4016.
Ctenophora flaveolata	Larva, pupa, general	Weyenbergh, 1872.
Ctenophora pectinicornis	Larva, pupa	Bouché, 1834:29–31.
Ctenophora pectinicornis	General	Fischer von Waldheim, 1838.
Ctenophora pectinicornis	Larva, pupa	Weyenbergh, 1872.
Ctenophora pectinicornis	General	Zetterstedt, 1851:4014.
Ctenophora pectinicornis	General	Kaltenbach, 1874:202.
Ctenophora festiva	Larva	Kaltenbach, 1874:631.
Ctenophora festiva	Larva	Czizek, 1911:48.
Ctenophora nigricoxa	Pupa	Lundström, 1906:7.
Ctenophora apicata	Larva, pupa	Johannsen, 1910:32–33.
Ctenophora angustipennis	Larva, pupa, general	Anthon, 1908.
Ctenophora angustipennis	Egg, larva, pupa, injury	Lovett, 1915.
Aeshnasoma rivertonensis	Larva	Johnson, 1906:1–2.
Aeshnasoma rivertonensis	General	Johnson, 1907–12 [1909]:115–116.
Tipulodina pedata	Pupa	De Meijere, 1911:64.
Holorusia rubiginosa	Larva, pupa, general	Kellogg, 1901, a and b.
Holorusia rubiginosa	Larva	Comstock and Kellogg, 1904: 54–62.
Prionocera fuscipennis	Larva, pupa, general	Malloch, 1915–17b:199–200.
Prionocera parri, supp (Palaearctic species)	Larva	Alexander, 1919 c.
Tipula caesia	General	Schiner, 1864:516.
Tipula dilatata	Larva, pupa	Beling, 1886:176.
Tipula dilatata	Larva, pupa	Czizek, 1913:169.
Tipula flavolineata	General	Staeger, 1840:23.
Tipula flavolineata	Larva, pupa	Beling, 1873 b:581–582.
Tipula flavolineata	Larva, pupa	Czizek, 1913:146.
Tipula fulvipennis	Larva, pupa	Beling, 1879:22–24 (as *lutescens*).
Tipula fulvipennis	Larva, pupa	Czizek, 1913:74.
Tipula hortensis	Larva, pupa	Beling, 1873 b:578–579.
Tipula hortensis	Larva	Gerbig, 1913:154–156.

Tipula hortulana	Larva, pupa, general	Beling, 1879:25; 1886:178–179.
Tipula hortulana	Larva, pupa, general	Czizek, 1913:96.
Tipula imbecilla	General	Loew, 1869:9.
Tipula irrorata[7]	Larva, pupa	Beling, 1873 b:586–587.
Tipula irrorata	Larva, pupa	Czizek, 1913:98–99.
Tipula lateralis	Larva, pupa	Beling, 1879:26–28.
Tipula lateralis	Larva	Gerbig, 1913:153–154.
Tipula lateralis	Larva, pupa	Czizek, 1913:128.
Tipula lateralis	General	Cameron, 1917:61.
Tipula lunata	Larva, pupa	Brocher, 1909.
Tipula luteipennis	Larva, pupa	Beling, 1886:181–182.
Tipula luteipennis	Larva, pupa	Czizek, 1913:143.
Tipula marmorata	Larva, pupa	Beling, 1886:182–183.
Tipula maxima	Larva, pupa	Beling, 1886:177–178 (as *gigantea*).
Tipula maxima	Larva	Gerbig, 1913:152–153 (as *gigantea*).
Tipula maxima	Larva, pupa	Czizek, 1913:70–71.
Tipula maxima	General	Wesenberg-Lund, 1915:335 (as *gigantea*).
Tipula micans[7]	Larva, pupa	Beling, 1886:183–184.
Tipula nigra	Larva, pupa	Beling, 1879:28–29.
Tipula nigra	Larva, pupa	Czizek, 1913:132.
Tipula nubeculosa	Larva, pupa	Beling, 1873 b:575–577.
Tipula nubeculosa	Larva, pupa	Czizek, 1913:113.
Tipula ochracea	Larva, pupa	Beling, 1873 b:582–583.
Tipula ochracea	Larva, pupa	Czizek, 1913:157.
Tipula oleracea	Larva, pupa	Del Guercio, 1914.
Tipula oleracea	General	Patterson, 1908.
Tipula pabulina	Larva, pupa	Beling, 1873 b:579–580.
Tipula pabulina	Larva, pupa	Czizek, 1913:86.
Tipula pagana	Larva, pupa	Beling, 1879:29–31.
Tipula paludosa	Larva, pupa	Beling, 1873 b:583–585.
Tipula paludosa	Larva	Gerbig, 1913:136–151.
Tipula paludosa	Larva, pupa	Czizek, 1913:136.
Tipula paludosa	Larva, pupa	Rennie, 1916; 1917.
Tipula parva, supp	General	Onuki, 1905.
Tipula peliostigma	Larva, pupa	Beling, 1879:33–34.
Tipula peliostigma	Larva, pupa	Czizek, 1913:159.
Tipula pruinosa	Larva, pupa	Beling, 1879:31–32; 1886:184.
Tipula pruinosa	Larva, pupa	Czizek, 1913:148.
Tipula rufina	Larva, pupa	Mik, 1882 a.
Tipula scripta	Larva, pupa	Beling, 1873 b:577–578.
Tipula scripta	Larva, pupa	Czizek, 1913:110.
Tipula selene	Larva, pupa	Beling, 1879:34–35.
Tipula selene	Larva, pupa	Czizek, 1913:160–161.
Tipula signata	Larva, pupa	Beling, 1879:32–33.
Tipula signata	Larva, pupa	Czizek, 1913:104.
Tipula simplex	General	Doane, 1908.
Tipula subnodicornis	Larva, pupa	Beling, 1886:185–186.
Tipula truncorum	Larva, pupa	Beling, 1879:24–25.

[7] *Tipula micans* is considered by Kertész and others as a synonym of *T. irrorata*, but Beling's descriptions indicate that he had two distinct species before him.

Tipula truncorum	Larva, pupa	Czizek, 1913:82.
Tipula unca	Larva, pupa, general	Beling, 1886:179–181 (as *longicornis*).
Tipula unca	Larva, pupa	Czizek, 1913:101–102 (as *longicornis*).
Tipula variicornis	Larva, pupa	Beling, 1886:173–174 (as *annulicornis*).
Tipula variicornis	Larva, pupa	Czizek, 1913:122–123.
Tipula variipennis	Pupa	Beling, 1873 b:580–581.
Tipula variipennis	Larva	Beling, 1886:186.
Tipula variipennis	General	Westhoff, 1879.
Tipula variipennis	Larva	Gerbig, 1913:131–136.
Tipula variipennis	Larva, pupa	Czizek, 1913:91–92.
Tipula vernalis	Larva, pupa	Beling, 1879:25–26.
Tipula vernalis	Larva, pupa	Czizek, 1913:120.
Tipula vittata	Larva, pupa	Beling, 1886:186–188.
Tipula vittata	Larva, pupa	Czizek, 1913:78.
Tipula winnertzii[8]	Larva, pupa	Beling, 1873 b:585–586; 1886:188–189.
Tipula winnertzii	Larva, pupa	Czizek, 1913:84–85.
(Nearctic species)		
Tipula abdominalis	Larva	Malloch, 1915–17 b:200–201 (as *Tipula* sp. 2).
Tipula arctica	Larva, pupa	Nielsen, 1910:57–59.
Tipula arctica	Larva, pupa	Alexander, 1919 c:18c, 19c.
Tipula bicornis	Larva, pupa	Forbes, 1890.
Tipula caloptera	Larva	Needham and Betten, 1901:575–576 (as *abdominalis*).
Tipula cunctans	Larva, pupa, general	Hyslop, 1910 (as *infuscata*).
Tipula cunctans	Larva, pupa	Malloch, 1915–17 b:204.
Tipula eluta	Larva, pupa, general	Hart, 1898 [1895]:212–214.
Tipula eluta	Larva, pupa	Malloch, 1915–17 b:203.
Tipula serta (?)	Pupa	Malloch, 1915–17 b:205.
Tipula trivittata	Larva, pupa	Greene, 1909.
Tipula trivittata	Pupa	Malloch, 1915–17b:204–205.
Tipula ultima	Pupa, general	Needham, 1903:280–281 (as *flavicans*).
Tipula ultima	General	Caudell, 1913 (as *flavicans*).
Habromastix cinerascens	General	Skuse, 1890:95.
Nephrotoma analis	Larva, pupa	Beling, 1886:172–173.
Nephrotoma analis	Larva, pupa	Czizek, 1911:70–71.
Nephrotoma cornicina	Larva, pupa	Beling, 1879:39–40 (as *iridicolor*).
Nephrotoma cornicina	Larva, pupa	Czizek, 1911:76.
Nephrotoma crocata	Larva, pupa	Beling, 1879:40–41.
Nephrotoma crocata	Larva, pupa	Czizek, 1911:87.
Nephrotoma lineata	Larva, pupa	Beling, 1879:42–43 (as *histrio*).
Nephrotoma lineata	Larva, pupa	Czizek, 1911:83–84.
Nephrotoma lunulicornis	Larva, pupa	Beling, 1879:41–42.
Nephrotoma lunulicornis	Larva, pupa	Czizek, 1911:61.
Nephrotoma maculata	Larva, pupa	Beling, 1879:36–37.
Nephrotoma maculata	Larva, pupa	Czizek, 1911:80–81.
Nephrotoma pratensis	Larva, pupa	Beling, 1886:175–176.

[8] Riedel (1913:25) considers *Tipula winnertzii* as a synonym of *T. truncorum*, but Beling's descriptions indicate that the larvae he had before him represented two distinct species.

Nephrotoma pratensis	Larva, pupa	Czizek, 1911:85–86.
Nephrotoma quadrifaria	Larva, pupa	Beling, 1879:37–39.
Nephrotoma quadrifaria	Larva, pupa	Czizek, 1911:66.
Nephrotoma ferruginea	Larva, pupa	Hart, 1898 [1895]:218–219.
Nephrotoma ferruginea	Larva, pupa	Malloch, 1915–17 b:206.

Tribe **Tipulini**

Subtribe **Dolichopezaria**

Genus **Dolichopeza** Curtis (Gr. *long* + *feet*)

1825 *Dolichopeza* Curt. Brit. Ent., p. 62.
1830 *Leptina* Meig. Syst. Beschr. Zweifl. Ins., vol. 6, pl. 65, fig. 10.
1846 *Apeilesis* Macq. Dipt. Exot., Suppl. 1, p. 8.

The genus Dolichopeza is a small group of flies including about a score of species, most numerous in the Oriental and Australian regions. The immature stages of the European *Dolichopeza albipes* Ström, a species that is very close to the American species *D. americana* Needm., have been described by Beling (1879, 1886). He found larvae in and beneath moss cushions covering the piles of waste copper slag in the Harz Mountains. On June 11, 1878, larval and pupal material was taken from a tussock of the Jungermanniales liverwort *Alicularia scalaris* Corda. The pupal period was found to be six days. Females were noted depositing their eggs in these hummocks, and small swarms of males were observed dancing near by. It appears that the larvae feed on the upper side of the moss cushion at night, withdrawing into the interior at other times. A larva was found in earth, which shows that these larvae are not dependent on mosses.

The larva is described by Beling (1886:189–191) as being about 12 millimeters long and 2.3 millimeters in diameter. The body is almost terete. The color is a rather bright green, the dorsum being marked with two zigzag dark brown stripes. The spiracular disk has but five lobes; the three dorsal lobes are long and narrow, the median tooth being formed by the apparent fusion of two teeth; the ventral lobes are very short, are tuberculate, and have a small, dark brown, triangular mark at the inner tip. There is a small dark cross-stripe at the base of each lateral lobe. The spiracles are small, are circular, and are separated by a distance equal to about one and one-half the diameter of one. Beneath each spiracle is a rather large, irregular, blackish brown spot. The anal gills are strongly protuberant. The pupa measures about 14.5 millimeters in length and 2.5 millimeters in diameter. The pronotal breathing horns

are directed straight outward and finally downward. The eighth segment has a circle of four dorsal, four ventral, and two pleural spines, which are finely bifid at their tips. The pupa is green, as is the larva, with similar angular dorsal stripes.

This is the only tipuline larva known to the writer with five lobes surrounding the spiracular disk. This feature is the more remarkable when this larva is compared with that of Oropeza, apparently closely related but with a normal tipuline appearance. The immature stages of other species of Dolichopeza and related genera will be of interest.

The resting positions of Dolichopeza are described on page 713 of this paper, and the striking dissimilarities to Oropeza noted. It may be that Oropeza is not so close to Dolichopeza as has been believed. Osten Sacken (1886:157) describes the mating of a European Dolichopeza, presumably *D. albipes,* as follows:

> I had occasion to observe the copula (in Heidelberg, July 26); the female was hanging down from some support to which it held on by its front legs; it bore the whole weight of the male, who was fastened to it merely by the forceps, hanging head downwards, with his legs stretched out. I have seen Bittacomorpha copulate in the same manner.

Genus **Oropeza** Needham (Gr. *mountain + feet*)

1908 *Oropeza* Needm. 23d Rept. N. Y. State Ent. (1907), p. 211.

Larva.— Form somewhat depressed. A strong tubercle on sides of body before spiracular disk. Spiracular disk surrounded by six lobes, the four dorsal ones slender, the ventral pair blunt. Anal gills blunt. Head capsule of the tipuline type. Mandible blunt, with about seven teeth. Hypopharynx five-toothed. Mentum seven-toothed. Coloration dark green.

Pupa.— Pronotal breathing horns elongate-cylindrical, slender. Mesonotum with a slightly elevated triangular area on either side of mid-dorsal line. Leg sheaths ending about on a level, or fore legs a little longer. Abdominal segments with two stout pleural spines; posterior annuli before margin with a transverse row of twelve or fewer spines.

Oropeza is a genus of crane-flies including ten described species, all of which occur in eastern North America with the exception of three Japanese forms. The flies are common beneath dark culverts and bridges, in outhouses, in crannies and crevices of rocky cliffs, beneath overhanging boulders along mountain streams, and in similar situations. The resting positions of the adult flies are discussed on page 712. Many species show a notable predilection for resting on spiders' webs. The immature stages of *Oropeza obscura* are spent in dry moss, as discussed below. Other species have been reared in sandy soil and in wet moss.

Oropeza obscura Johns.

1909 *Oropeza obscura* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 122.

Mr. Hyslop has sent to the writer, at various times during the past two or three years, larvae of *Oropeza obscura*. Numerous larvae and one pupal skin were found under dry moss (*Hedwigia albicans* [Web.] Lindb.) on rocks in the South Mountains, Maryland, on November 4, 1916, by H. L. Parker. They were associated with the larvae of a dascillid beetle, *Eurypogon niger* (Melsh.). Additional specimens were found in a decaying log, but the preferred habitat seems to be beneath moss. The dark green larvae are very sluggish.

Larva.— Length, 11–12 mm.
Diameter, 1.7–1.8 mm.

Color dark brownish green, ventral surface clearer green.

Form depressed; body short and stout. Dorsum covered with small, blackened points, producing the dark color of this region of the body. Segments much wrinkled, especially on basal ring. On each side of penultimate segment a stout tubercle which simulates dorsal lobes of spiracular disk. Spiracular disk (Plate LXXXVI, 469) moderate in size, surrounded by six fleshy lobes, dorsal pair short and slender, lateral pair long and slender, ventral pair very short and blunt; ventral lobes sparsely fringed with short, black hairs, and with a pale apical area bearing a sensory bristle; inner face broadly suffused with brown; at base of other lobes similar but smaller triangular brown marks; a dusky area ventrad of spiracles. Spiracles large, placed obliquely. Anal gills four, large and blunt, pale yellow.

Head capsule of the massive tipuline type. Labrum broad, with a short, blunt lobe on either side; median epipharyngeal region with dense rows of stout setae and two small papillae on margin; lateral lobes with about four or five sensory bristles or papillae of various sizes. Mentum (Plate LXXXVI, 467) seven-toothed, median point long and slender, a prolongation of outer mental plate. Hypopharynx (Plate LXXXVI, 468) five-toothed, the three intermediate teeth the largest, lateral tooth on either side small. Antenna slender, cylindrical, with apical segment very reduced. Mandible rather slender, with about seven blunt teeth on margin. Maxilla with cardo large, triangular, with two setiferous punctures, the outermost very large and hyaline and with two long, powerful setae; lobes of maxilla fringed with dense hairs; palpus short, disklike, with a large group of tiny hyaline papillae at apex.

Pupa.— Length of cast skin, about 12 mm.

Coloration brown; pronotal breathing horns dark blackish brown. (It is possible that the pupae when alive are dark green in color, like the larvae.)

Labrum triangular. Labial lobes large, separated by apex of labrum. Sheaths of maxillary palpi short and stout, apex recurved to beyond midlength. Antennal sheaths moderately elongated. Pronotal breathing horns elongate, slender, cylindrical, tips a little expanded. Mesonotum on either side of median line with a large, roughly triangular, reticulated area which is slightly elevated, with apex of triangle directed toward mid-dorsal line. Mesonotum

transversely wrinkled. Metanotum (Plate LXXXVI, 470) near anterior margin with a transverse row of setiferous punctures, there being four on either side, the intermediate ones with two setae. Wing sheaths reaching base of third abdominal segment. Leg sheaths reaching beyond midlength of fourth abdominal segment, fore legs a little the longest, hind legs a little the shortest.

First abdominal segment on dorsum somewhat similar to metanotum, with a transverse row of four punctures at about midlength, the lateral ones with two setae; remaining abdominal segments (Plate LXXXVI, 471) subdivided into approximately equal basal and posterior rings; on tergites, posterior ring with a transverse row of spines, basal ring unarmed; on sixth tergite, where best developed, spines on posterior ring numbering about twelve, with a seta at each end of the row and two others interspersed; on anterior tergites, spines very small; on seventh tergite spines large, elongated; on eighth tergite four powerful spines in transverse alinement; on pleurites, a strong spine on each ring, that of basal ring deeply bifid and with a strong seta in notch thus formed; posterior ring with a single spine bearing a long seta on its face; on sternites, condition generally similar to that on tergites, the spines a little more prominent but of about the same number, these spines slender at their slightly curved tips and lacking on sternites 2 to 4. Female cauda (Plate LXXXVI, 472 and 473) with acidothecae elongate, contiguous, on either side of tergites at base with a powerful incurved hook; posterior margin of eighth tergite with four spines, lateral pair a little the larger; ventral side at base with a median protuberance bearing two powerful lateral lobes and two smaller chitinized spines which are directed caudad and ventrad; base of segment 8 with a crossrow of eight spines; posterior ring of segment 8 with a powerful spine at lateral end.

Nepionotype.— South Mountains, near Myersville, Maryland, March 31, 1916.
Neanotype.— Hagerstown, Maryland, May 9, 1916; cast pupal skin in collection of United States National Museum.
Paratypes.— Larvae from type locality.

Genus **Brachypremna** Osten Sacken (Gr. *short* + *trunk*)

1886 *Brachypremna* O. S. Berl. Ent. Ztschr., vol. 30, p. 161.

Larva.— Unknown.

Pupa.— Antennal segments enlarged at base. Antenna short. Sheaths of maxillary palpi short, not recurved at tips. Pronotal breathing horns short, slender, finely annulated. Mesonotum with eight prominent tubercles. Leg sheaths reaching beyond midlength of fourth abdominal segment, fore tarsi very short, other tarsi subequal in length. Abdominal segments each with four slender spines on posterior ring of both sternites and tergites, just before posterior margin; two pleural spines; eighth segment of male with four prominent, spinous lobes.

Brachypremna is a small genus, including but nine recent species found in the Austral and Tropical regions of the New World. *Brachypremna eocenica* Meunier is described from the Baltic amber. The flies of the best-known species, *B. dispellens,* are known in parts of the Southern

States as "weavers." They frequent rather shady places and have a remarkable dance over three or four feet of vertical space, whence the name "king of the dancing tipulids" given them by Johnson. This species is the only one whose immature stages are at all known.

Brachypremna dispellens (Walk.)

1860 *Tipula dispellens* Walk. Trans. Ent. Soc. London, n. ser., vol. 5, p. 333–334.
1886 *Brachypremna dispellens* O. S. Berl. Ent. Ztschr., vol. 30, p. 162.

Brachypremna dispellens is the most widely distributed species of the genus. It ranges from New Jersey southward thru North America, and thru South America as far as Argentina. A larva found by R. C. Shannon in a rotten log by a stream near Washington, D. C., on April 23, 1913, was placed in rearing and emerged in May as an adult male of this species. The badly mutilated pupal skin was preserved and is here described. No part of the larva was preserved.

Pupa.— Length of cast pupal skin, about 18 mm.

Coloration brownish yellow; abdomen with a broad brown sublateral stripe on both ventral and dorsal segments; each of pleural spines set in a brown spot.

Head small. Antennal spines very large and crowded at base, soon passing into the short, slender flagellum. Labrum (Plate LXXXVII, 474) blunt. Labial lobes closely approximated, so as to appear as a single large, transversely rectangular lobe at end of labrum. Sheaths of maxillary palpi short, not recurved at tip. Pronotal breathing horn (Plate LXXXVII, 475) small, slender, curved, ringed with fine annuli, tapering gradually to the small apex; margin of apex set with breathing pores. Mesonotum with eight conspicuous, blunt, naked tubercles; the four intermediate tubercles larger, arranged in the form of a trapezoid; anterior median pair high, conical, located rather close to mid-dorsal line. Wing sheaths reaching end of second abdominal segment. Leg sheaths (Plate LXXXVII, 476) extending beyond mid-length of fourth abdominal segment; fore legs very short, ending opposite base of third tarsal segment of other legs.

Abdominal tergite 1 with a pair of long, slender spines before posterior margin; segments 2 to 7 subdivided into a basal and a posterior ring, the latter with a transverse row of four long, slender spines before posterior margin, the seventh tergite with about six such spines; sternites similar, with four spines on posterior ring; pleurites with a slender spine on basal and posterior ring; at base of posterior ring between spines, an indistinct, slightly protuberant spiracle. Male cauda (Plate LXXXVII, 477) narrowed, small, valves blunt; on dorsal side near base four conspicuous lobes, each terminating in a slender, chitinized spine; a small acute spine on sides of ninth segment at base.

Neanotype.— Cast pupal skin, Washington, D. C., May, 1913 (in collection of United States National Museum).

Subtribe **Ctenophoraria**

Genus **Ctenophora** Meigen (Gr. *comb + to bear*)

1800 *Flabellifera* Meig. Nouv. Class. Mouch., p. 13 (*nomen nudum*).
1803 *Ctenophora* Meig. Illiger's Mag., vol. 2, p. 263.
1910 *Phoroctenia* Coq. Proc. U. S. Nat. Mus., vol. 37, p. 589.

Larva.— Body opaque, integument rather thick. Spiracular disk surrounded by six lobes.

Pupa.— Sheaths of maxillary palpi recurved. Pronotal breathing horns long and slender Two spines on mesonotum. Fore and middle tarsi subequal, a little shorter than hind tarsi. Ventral abdominal segments with six to eight spines.

Ctenophora is a small genus including about sixteen nominal species found thruout the Holarctic region. The larvae and the pupae occur in decaying wood. The early stages have long been known, having been described by Réaumur and De Geer.

In Europe, *Ctenophora flaveolata* (Fabr.) is described and figured by Réaumur (1740) and by Weyenbergh (1872). *C. pectinicornis* (Linn.) is described or mentioned by Bouché (1834), by Fischer von Waldheim (1838), by Zetterstedt (1851:4014), by Weyenbergh (1872), and by Kaltenbach (1874). *C. festiva* Meig. was reared by Kaltenbach (1874:631) from larvae in decayed beech stems. *C. nigricoxa* Lundst. (*Malpighia vittata* Meig., auct. Frey) was reared by Lundström (1906:7) from pupae in rotten birch stumps. The immature stages of the various European species of Ctenophora are described as living in the wood of various trees such as willow (Salix), birch (Betula), cherry (Prunus), and other hardwood species.

In North America, *C. apicata* is described by Johannsen (1910) from elm (Ulmus), and *C. angustipennis* Loew by Anthon (1908) in alder (Alnus) and in poplar (Populus). The latter species is recorded also as injuring prune trees (Prunus) in Oregon, by Lovett (1915), who gives an excellent account of all stages and the type of injury done. The female lays from 200 to 400 eggs, which hatch in from nine to seventeen days and the larvae tunnel into the surrounding dead wood. Here they feed and grow, reaching maturity the following spring. Pupation takes place in the burrows, the pupal stage requiring about ten days. Osten Sacken (1877:211) supposed that the larvae live in the stumps of redwood (Sequoia), but this has never been confirmed.

Ctenophora apicata O. S.

1864 *Ctenophora apicata* O. S. Proc. Ent. Soc. Phila., vol. 3, p. 46.

The larvae and the pupae of *Ctenophora apicata* that were described by Johannsen (1910) have been studied by the writer in the collection of the Maine Agricultural Experiment Station. They were collected at Orono, Maine, on June 23, 1909, by Dr. William C. Woods. In 1913 the writer examined the stump from which they were taken, and found a few cast pupal skins.

The notes here given are taken partly from Dr. Johannsen's description and partly from the original material.

Larva.— Length, about 30 mm.

Color white. Body stout, cylindrical. Antenna cylindrical, with an apical papilla. On dorsum of head behind antennae, a slender, flexible spine. Spiracular disk surrounded by six lobes, dorsal and lateral pairs slender, finger-like; ventral pair blunt.

Pupa.— Length, 25–27 mm.
Length of breathing horns, 3 mm. additional.
Width, d.-s., 5.2 mm.
Depth, d.-v., 5 mm.

Pupa somewhat similar to that of Tanyptera, differing as follows: Form stout; abdomen a little depressed. Sheaths of maxillary palpi strongly recurved at tips. Pronotal breathing horns long and slender. Mesonotum with a prominent tuberculate spine on either side of median line. Legs short, ending before tip of third abdominal segment; tarsal sheaths ending about on a level, or those of hind legs a very little longer. Abdominal segments 5 to 7 with six to eight spines. Female cauda with six powerful ventral spines or tubercles and two dorsal tubercles on either side. Valves of ovipositor short, tergal valves a little longer than sternal valves.

Nepionotype.— Orono, Maine, July, 1909.
Neanotype.— Orono, Maine, July, 1909.
Paratypes.— Numerous pupae in collection of Maine Agricultural Experiment Station.

Genus **Dictenidia** Brullé (Gr. *double + comb*)

1833 *Dictenidia* Brullé. Ann. Soc. Ent. France, vol. 2, p. 401–402.
1856 *Ceroctena* Rond. Dipt. Ital. Prodr., vol. 1, p. 186.
1863 *Dicera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 216.

Dictenidia is a genus of Palaearctic crane-flies including three species, of which one is European and the others are Japanese. The genotype, *Dictenidia bimaculata* Brullé, is very well known. The immature stages are described or mentioned by Bouché (1834), by Zetterstedt (1851), by Weyenbergh (1872), by Beling (1873 b), by Czizek (1913), and by other investigators. Beling found the larvae in decaying birch (Betula). He describes the larvae as being grayish yellow, with four spiracular lobes. The pupal duration is seven days. Osten Sacken (1886:173–175) states that he has often found larvae in the wet detritus underneath the bark

of decaying trees. The larvae are much closer to Ctenophora than to Tanyptera, the skin being tough and opaque, with a fine pubescence, and the spiracular disk consisting of small but distinct lobes. The pupae likewise are similar to those of Ctenophora, having the pronotal breathing horns elongate, five spines on abdominal sternites 3 to 6, and four spines on tergites 2 to 7.

Genus **Tanyptera** Latreille (Gr. *extend + wing*)

1805 *Tanyptera* Latr. Hist. Nat. Crust. et Ins., vol. 14, p. 286.
1832 *Xiphura* Brullé. Ann. Soc. Ent. France, vol. 1, p. 206.

Larva.— Integument very thin, with numerous setae, those on dorsum very small. Spiracular disk with lobes practically lacking. Spiracles large, lying exposed on the face of last segment. Anal gills bluntly rounded. Mandible small, with one dorsal and one ventral tooth. Antenna cylindrical, capped with an apical cone. Mentum with seven to nine teeth.

Pupa.— Cephalic crest lacking. Sheaths of maxillary palpi not recurved at tips. Pronotal breathing horns large, broadly flattened, margin deeply crenulated. Mesonotum with two blunt tubercles. Abdominal segments with six to ten spines on tergites, three to five spines on sternites.

Tanyptera is a small genus including about twelve nominal species whose limits and relationships are still but little understood. The immature stages are spent in the decayed or partly decayed wood of various deciduous trees.

In Europe, *Tanyptera atrata* (Linn.), the genotype, was found by Perris (1840) and by De Rossi (1882) in decaying alder (Alnus) stems. Nördlinger (1848) found the same species in linden (Tilia) and in poplar (Populus). It has also been taken in oak (Quercus), beech (Fagus), birch (Betula), and other hardwood species. Gerbig (1913) discussed the variety *ruficornis* Meig. under the name *Ctenophora flavicornis*.

In America, Malloch (1915–17 b: 194–195) describes *T. fumipennis* (O. S.) from a much-decayed chestnut log (Castanea), and later (1919) in basswood (Tilia), where the species was associated with larvae of *Xylota fraudulosa* Loew and *Chalcomyia aerea* (Loew), of the family Syrphidae. *Tanyptera frontalis*, discussed below, was found in red maple (Acer).

Tanyptera frontalis (O. S.)

1864 *Ctenophora frontalis* O. S. Proc. Ent. Soc. Phila, vol. 3, p. 48.

The writer found numerous larvae of *Tanyptera frontalis* in a fallen log of red maple (*Acer rubrum* Linn.) near Beebe Lake, Ithaca, New York, on March 22, 1913. Larvae of several sizes were found. They were working in wood which was well preserved, not entirely sound but still so hard that it had to be cut with a hatchet. The larvae pupated in April. A small male emerged on May 1.

Other larvae of Tanyptera were found in a hickory log (*Carya* sp.) at Sandy Landing, Virginia (opposite Plummers Island), on September 9, 1913. Detailed drawings of the larval structure made by Dr. Böving are in the collection of the United States National Museum.

Larva.— Length, 30–35 mm.
Diameter, 7–7.2 mm.

Coloration, pale yellowish white.

Form terete, very stout. Integument thin. Numerous long black setae on segments (Plate LXXXVIII, 482), arranged in transverse rows before posterior margin; setae of dorsum (Plate LXXXVIII, 481) very tiny, one on either side of median line; a pair of setae laterad of these and in alinement; setae on pleural region very long and delicate; on thoracic segments, setae at about midlength; on abdominal segments, setae closer to posterior margin; mid-ventral setae very tiny, four in number, on thoracic segments at about midlength, forming a stiff pencil on sides of venter, with two small setae between; laterad of these four intermediate setae, a group of three setae, two long and one very short; ventral setae lying at a level posterior to that of pleural setae. Spiracular disk (Plate LXXXVIII, 483) with lobes practically lacking, the two large, oval spiracles lying exposed on truncated end of last segment; above and laterad of each spiracle, a small, blunt lobe with a blackened mark and three long setae; below spiracles, two narrow black lines representing the two ventral lobes; a small pencil of setae below each of these marks, and each mark having a sensory bristle; three or four long setae on sides of spiracular disk. Spiracles with small middle piece black, ring yellowish brown; spiracles separated by a distance a little greater than diameter of one. Anal gills four, bluntly rounded, very protuberant and evidently formed for propulsion. (In older specimens the anal gills are minutely roughened and are darker in color.)

Head capsule of the massive tipuline type. Labrum rather broad; median epipharyngeal region with a small brush of hairs surrounding two sensory setae; lateral lobes large, on their ventral face densely hairy, surrounding four sensory setae and a flattened hyaline peg. Mentum (Plate LXXXVIII, 478) rather small, broadly rounded, anterior margin with seven or nine teeth, in the latter case the outermost tooth on either side very blunt and reduced, the median tooth long and flattened. Antenna (Plate LXXXVIII, 479) short-cylindrical; apical papilla very small, hyaline, conical, with surface sculptured; in addition to this cone, three or four small hyaline sense pegs; the usual auditory organ located at about midlength of segment. Mandible (Plate LXXXVIII, 480) small, with one dorsal and one ventral tooth in addition to the apical point, ventral tooth flattened and with margin crenulated; a stout seta at heel of mandible; prostheca an elongated cone, situated at base

of mandible. Maxilla rather small, simple; palpus large, antenniform, with apex bluntly rounded; inner lobe densely covered with short, stout setae surrounding a powerful bristle and a small brown sensory organ.

Pupa.— Length, 30–33 mm.
Width, d.-s., 5–6 mm.
Depth, d.-v., 5.5 mm.

Coloration pale yellow; pronotal breathing horns liver-colored. (In older specimens the thorax and appendages are dark-colored, and the abdomen has broad brown sublateral stripes.)

Head rather small, cephalic crest lacking. Antenna stout, rather elongate, extending far beyond ends of palpi, segments angulated. Clypeus and labrum tumid, transversely wrinkled. Labial lobes slender, divergent. Sheaths of maxillary palpi rather slender, tips curved but not recurved (Plate LXXXVIII, 485). Pronotal breathing horn (Plate LXXXVIII, 486) large, broadly flattened, slightly incurved, broader at apex than at base, deeply furrowed up middle of outer face, the broad margin thus formed deeply wrinkled to crenulate. Mesonotum large, transversely wrinkled, with two blunt tubercles provided with short setae (Plate LXXXVIII, 484). Wing sheaths small, reaching end of second abdominal segment. Leg sheaths ending before tip of third abdominal segment; fore tarsi very short, hind tarsi the longest, those of middle legs intermediate.

First abdominal tergite with two spines; segments 2 to 7 broad, divided into the usual basal and posterior rings; second segment on posterior ring with four spines; segments 3 to 6 with six to ten spines, the intermediate ones usually smaller; segment 7 with four spines; pleurites with a spine on each ring; sternites with similar arrangement to that of tergites, but spines usually fewer in number, segments 3 and 4 with only a single widely separated spine on each side, segments 5 and 6 with four or five spines, segment 7 with three spines; segment 8 has four small spines between the large lateral ones described below. Male cauda blunt, dorsal lobes very divergent, ending in sharp, chitinized points. Female cauda (Plate LXXXVIII, 487) with tergal valves elongate, narrowed to the moderately acute tips; sternal valves similar in shape but smaller; lateral lobes of ninth segment directed caudad and laterad, at tips running out into chitinized points; two small setae before tips; segment 8 with a powerful lateral lobe on either side, each terminating in a chitinized point; posterior lateral angles of segment produced into slender, blunt points.

Nepionotype.— Ithaca, New York, March 22, 1913.
Neanotype.— May 1, 1913. No. 11–1913.
Paratypes.— Four larvae and two pupae with types.

Subtribe **Tipularia**

Genus **Longurio** Loew (Lat. *a tall man*)

1869 *Longurio* Loew. Berl. Ent. Ztschr., vol. 13, p. 2.

Larva (supposition).— Body massive. Integument semi-transparent. Form clearly depressed. Spiracular disk surrounded by six lobes, dorsal pair very small, ventral pair very long; ventral and lateral lobes provided with but few setae at and near tips; spiracular

disk and lobes unmarked. Spiracles small. Anal gills branched. Mandible small, with but a single dorsal and ventral tooth in addition to apical point. Mentum with nine teeth. Hypopharynx five-toothed.

Pupa.— Antenna short, ending opposite tips of maxillary palpi. Sheaths of maxillary palpi not recurved at tips. Mesonotum unarmed. Pronotal breathing horns very long and slender, one, at least, about half length of body. Wings showing clearly the characteristic venation of Longurio. Abdomen elongate, posterior ring of individual segments with short, stout spines, including a few on pleurites; dorsum of eighth segment with four powerful lobes.

Longurio is a small genus including about ten described species, of which two occur in eastern North America. The genotype, *Longurio testaceus*, is the best-known species locally. The immature stages of this species are here discussed for the first time. They are spent in sand or sandy earth. The branched anal gills of the larva, and the excessively elongate breathing horns of the pupa, are notable features.

Longurio testaceus Loew

1869 *Longurio testaceus* Loew. Berl. Ent. Ztschr., vol. 13, p. 2.

Longurio testaceus is probably the largest crane-fly in North America, the females exceeding the better-known Holorusia of the Western States. The adult flies are difficult to capture, being very wary. When the insect is at rest the body generally hangs perpendicularly, with the wings folded incumbent over the abdomen.

On November 9, 1916, Mr. Hyslop sent the writer two living larvae which are referred with little doubt to this species. They were found in wet sand in a bog on the top of South Mountains, near Myersville, Maryland. The larvae were very restless, the head capsule being constantly exserted and withdrawn. Waves of contraction start from the posterior end of the body and pass toward the head. A large pupa taken by Dr. J. C. Bradley at Tallulah Falls, Georgia, on June 17, 1910, undoubtedly belongs to this species, the venation being clearly apparent on the wing pad. An additional cast pupal skin is in the collection of the United States National Museum.

Larva (supposition).— Length, 31 mm. contracted, 58 mm. extended.
Diameter, 11–12.5 mm.

Color whitish, subhyaline; thoracic segments more yellowish; in life the brown food contents showing clearly thru abdomen.

Form very depressed, lateral folds prominent; body very stout and fleshy. Skin very thin and semitransparent, showing internal organs within, practically destitute of pubescence;

a few short setae on body, especially on thoracic segments. Spiracular disk (Plate LXXXIX, 490) large, flattened, surrounded by six lobes; dorsal pair very small, represented by two short, conical protuberances; lateral and ventral lobes slender, the latter a little the longer, each with three or four long, delicate setae at tip and two or three others before tip on outer face; a long seta on margin of disk between dorsal and lateral lobes; spiracular disk and lobes entirely unmarked with darker. Spiracles small, circular, stigmal rings very narrow; spiracles separated by a distance equal to about three times diameter of one. Anal gills four, large, pinnately branched, each gill with six lateral branches.

Head capsule massive, of the tipuline type. Labrum with a distinct, densely hairy lobe on either side. Mentum (Plate LXXXIX, 488) large; anterior margin with nine slender teeth, median one the longest, outermost teeth on either side blunt, flattened, evidently formed by fusion of two teeth. Hypopharynx (Plate LXXXIX, 489) five-toothed; teeth blunt, the three middle ones larger, the lateral tooth on either side a little smaller. Antenna long and slender, cylindrical; apex blunt and without distinct sense pegs or setae. Mandible small, with a large conical dorsal tooth and a single flattened ventral tooth in addition to apical point; prostheca distinct. Maxilla small; palpi large, cylindrical, truncated at apex and with a circular auditory plate near end; inner lobe of maxilla with abundant elongate setae.

Pupa.— Length, 42–45 mm.
Length of longest breathing horn, 18–19 mm. additional.
Width, d.-s., 3 mm.
Depth, d.-v., 4.2 mm.

Color dark brown; pronotal breathing horns paler at tips; mesonotum chestnut brown; abdominal segments indistinctly ringed with pale and darker.

Front between antennal bases swollen, finely tuberculate but without distinct setae. Antenna very short, ending opposite tips of maxillary palpi. Labrum large. Sheaths of maxillary palpi not recurved at tips. Mesonotum unarmed, with fine transverse wrinkles. Pronotal breathing horns (Plate LXXXIX, 491) very long and slender, the right one, at least, exceedingly elongate, with tip expanded. (The left breathing horn was broken before the apex in both the pupae studied; it was almost as long as the right horn, and may, of course, have been longer.) Wing pads reaching end of second abdominal segment; characteristic venation of genus showing clearly on sheath. Leg sheaths long, extending to beyond mid-length of fourth abdominal segment; fore legs shorter than the others.

Abdomen elongate. Abdominal segments 2 to 7 near posterior margin with a transverse row of short, stout spines which are interrupted only near pleura; pleural area with four or five spines; ventral and dorsal segments with numerous spines; dorsal row of spines more distant from posterior margin of segment than the other areas; dorsum of eighth segment with four powerful, chitinized lobes directed dorsad and caudad; posterior margin of these lobes with about five or six small teeth; two spines near base of pleural region on segment 8. Male cauda consisting of two blunt sheaths, lying between posterior pair of lobes described above.

Larva.— South Mountains, near Myersville, Maryland, November 6, 1916.
Neanotype.— Tallulah Falls, Georgia, June 17, 1910.
Paratype.— Cabin John Bridge, Maryland, May 31, 1900.

Genus **Aeshnasoma** Johnson (Gr. *a dragon fly + body*)

1909 *Aeshnasoma* Johns. Proc. Bost. Soc. Nat. Hist., vol. 34, p. 115–116.

Aeshnasoma is a monotypic genus found in northeastern North America. It is unquestionably close to Longurio and may be congenerous with it. The type, *Aeshnasoma rivertonensis* Johns., is apparently very local in its distribution.

Johnson (1906:1–2) described an unknown tipuline larva which undoubtedly pertains to this species. The larva was found on June 10, 1900, in a cold spring at Riverton, New Jersey. It was brought into the laboratory but could not be reared, the change from the cold spring (about 60° F.) to warmer waters being fatal. The larva when fully extended measured about 45 millimeters in length. It was yellowish white in color and was translucent, the alimentary canal with its contents being clearly visible thru the thin skin. Johnson describes and figures the peculiar branched anal gills (Plate LXXXIX, 492) of this genus. The larva was doubtfully referred to Longurio, the adults of Aeshnasoma being undescribed at that time.

In a later paper (1907–12 [1909]:115–116) Johnson mentions the taking of several more larvae in 1902, and, on July 20, the capture of the adult flies on which the genus and species are based.

The only larva that was preserved was kindly sent to the writer for study by Mr. Johnson. It is undoubtedly very close to Longurio, both genera showing the same peculiar spiracular disk and the branched anal gills, a condition that is found nowhere else in the Tipulidae so far as is known to the writer.

Genus **Holorusia** Loew (derivation obscure)

1863 *Holorusia* Loew. Berl. Ent. Ztschr., vol. 7, p. 1.

Larva. — Spiracular disk surrounded by six moderately elongate lobes fringed with long hairs; inner face of lateral and ventral lobes with capillary black lines· disk between spiracles dusky. Anal gills six. Mandible small, with a single dorsal and ventral tooth in addition to apical point. Antenna with a conical apical papilla. Mentum seven-toothed. Hypopharynx six-toothed.

Pupa. — Sheaths of maxillary palpi recurved at tips. Pronotal breathing horns rather short and stout, the long apices flattened. Armature of abdominal segments almost as in Prionocera, but the posterior rows of spines more numerous (fourteen to twenty-four); pleurites with three spines, the two on posterior ring situated one behind the other. Cauda with six stout dorsal lobes.

Holorusia is a small genus (about ten species) of New World crane-flies, only one of which—the genotype, *Holorusia rubiginosa* — is Nearctic. This species and Longurio are the largest Nearctic crane-flies. The anatomy of the "giant crane-fly" has been described in some detail by Kellogg (1901, a and b) and by Comstock and Kellogg (1904). The immature stages are spent in moist earth. The genus is undoubtedly closely related to Prionocera, and, presumably, to the Old World genus Ctenacroscelis Enderlein.

Holorusia rubiginosa Loew

1863 *Holorusia rubiginosa* Loew. Berl. Ent. Ztschr., vol. 7, p. 1.
1888 *Tipula (Holorusia) grandis* Bergr. Ent. Tidskr., vol. 9, p. 140.

Holorusia rubiginosa is widely distributed thruout the western United States and Canada. A number of larvae were taken by H. Morrison near Stanford University, California, on February 22, 1915. They were shipped to the writer at Ithaca, New York, where the species was reared. The massive larva is used for purposes of dissection in the entomological courses at some of the western universities.

Larva.— Length, 50–60 mm.
Diameter, 6.2–6.4 mm.

Coloration, dark greenish brown.

Form stout, subterete. Integument covered with dense, short, erect, black hairs. A few weak and delicate setae, two on dorsum and on venter of each abdominal segment; two long setae on lateral margins of posterior rings. Spiracular disk (Plate XC, 496) moderately large, surrounded by six stout, elongate lobes which are similar to those of Prionocera but are stouter and less digitiform; ventral lobes a little the longest, dorsal lobes a little the shortest; all the lobes capable of close approximation, completely protecting spiracles; lobes fringed with long black hairs which are longest near apices, shorter between lobes; ventral and lateral lobes with a delicate black line down inner face, these lines barely indicated on dorsal lobes; remainder of disk and lobes dusky. Spiracles very large, circular, separated by a distance a little less than diameter of one. Anal gills six, short, slender, the two anterior gills of either side united basally, posterior pair simple.

Head capsule of the usual massive tipuline type, prefrons running caudad as a narrow point, lateral plates broad. Labrum broad, with a densely hairy lobe on either side. Mentum (Plate XC, 493) with a prominent median point; behind it on either side three flattened teeth, the innermost the broadest, the middle tooth more acute, the outermost formed by fusion of two small teeth. Hypopharynx (Plate XC, 494) about six-toothed, the intermediate teeth with a large notch between. Antenna (Plate XC, 495) with basal segment very long and slender; principal apical papilla conical; a number of small hyaline sense pegs. Mandi-

ble slender, with only two teeth, a stout dorsal tooth and a single flattened ventral tooth. Maxilla small, lobes covered with short, dense hairs.

Pupa.— Length, 32 mm.
Width, d.-s., 5 mm.
Depth, d.-v., 5 mm.

Color brown; flattened lateral margins of abdomen broadly yellowish.

Thorax terete; abdomen depressed, with lateral margins flattened, carinate. Cephalic crest represented by two low, parallel ridges, provided with one or two tiny setae. Labrum large, tumid, transversely wrinkled, the blunt apex completely separating the diamond-shaped labial lobes. Maxillary palpi stout, extreme tip recurved. Antenna moderately elongated, extending some distance beyond maxillary palpi. Pronotal breathing horns rather short and stout, finely ringed, the rather long tips flattened, about equal to one-fifth length of entire organ. Mesonotum convex (Plate XC, 497), with transverse anastomosing wrinkles; on either side of median line behind, a blunt tubercle. Wing sheaths reaching end of second abdominal segment. Leg sheaths extending just beyond base of fourth abdominal segment; fore tarsi short, middle tarsi a little longer than hind tarsi.

Abdominal segments with the usual basal and posterior rings; armature almost as in Prionocera; tergites with posterior row of spines numbering between twenty and twenty-four on intermediate segments, near anterior lateral angle two spines, basal ring unarmed; pleurites with one setiferous spine on basal ring and two similar spines on posterior ring, one placed considerably behind the other; sternites armed similarly to tergites, but the posterior row of spines larger and somewhat fewer in number (fourteen to eighteen); posterior ring on either side median line near base with two spines, the innermost very large and powerful. Male cauda with ventral lobes blunt, each armed with a slender black spine near posterior margin; dorsal surface of cauda almost as in Prionocera, armed with six stout lobes, which here are shorter and stouter, with tips abruptly narrowed; lateral margin of segment 8 with a stout lobe on either side, each terminating in a cylindrical spine. Female cauda similar to male cauda, dorsum with the same six lobes; acidothecae short, tergal valves slightly exceeding the more blunt sternal valves.

Nepionotype.— Stanford University, California, February 27, 1915.
Neanotype.— April 5, 1915.
Paratypes.— Larvae and pupae with types.

Genus **Prionocera** Loew (Gr. *saw* + *horn*)

1844 *Prionocera* Loew. Stett. Ent. Zeit., vol. 5, p. 170.
1863 *Stygeropis* Loew. Berl. Ent. Ztschr., vol. 7, p. 298.

Larva.— Spiracular disk surrounded by six long, finger-like lobes fringed with long, delicate hairs; each lobe with a capillary black line down middle of inner face. Spiracles large. Anal gills unbranched. Mentum seven- to nine-toothed. Hypopharynx five-toothed. Mandible with about two dorsal and three ventral teeth.

Pupa.— Maxillary palpi recurved at tips. Pronotal breathing horns very elongated, unequal, the longer one about half length of body; horns at tips split into long flaps. Abdominal tergites with a posterior transverse row of fifteen or fewer spines, and two small spines

near anterior lateral margin of posterior ring; pleurites with a spine on basal ring and two transverse spines on posterior ring. Cauda with six strong dorsal lobes.

Prionocera is a small genus (about a dozen species) of usually far northern flies of somber coloration. The only species found in eastern North America is *Prionocera fuscipennis*, discussed below. The immature stages are somewhat similar to those of Holorusia. The apparent similarity of the pupa to that of Longurio is probably not indicative of a very close relationship.

The immature stages have been discussed but little in the literature. The "Tipula sp. No. 1" of Malloch (1915–17 b: 199–200) refers to *P. fuscipennis*. The immature stages of a species supposed to be *P. parri* (Kirby) have been discussed and figured by the writer in his report on the Canadian-Arctic Tipulidae (Alexander, 1919 c: 19c–20c).

The name *Stygeropis* has been in use for many years under the belief that the earlier name *Prionocera* was preoccupied in the Coleoptera. Dr. Bergroth states that this is not so and that Prionocera should be used.

Prionocera fuscipennis (Loew)

1865 *Stygeropis fuscipennis* Loew. Berl. Ent. Ztschr., vol. 9, p. 129.

C. H. Kennedy found two cast pupal skins among Sparganium stems in Ringwood Hollow, Ithaca, New York, on November 20, 1916. Several larvae had been found here in the preceding July, and some others were found on June 4, 1917 (No. 106–1917), in a cat-tail swamp near Bool's hillside, Ithaca, where they were associated with the characteristic helophytic crane-fly fauna (Bittacomorpha, *Rhamphidia flavipes*, *Pseudolimnophila luteipennis*, *Pilaria recondita*, *Tipula tricolor*, and other species). Malloch's material was taken in Wisconsin in May. Dr. Needham has reared the species near Lake Forest, Illinois.

Larva.— Length, 18–22 mm.
Diameter, 2–2.2 mm.

Coloration dark brown, in some cases with a pale dorso-median stripe.

Form terete, tapering gradually to anterior end of body. Segments with several scattered elongate setae. Spiracular disk (Plate XCI, 502) surrounded by six long, finger-like lobes which are delicately fringed with long hairs; ventral lobes considerably the longest; lateral lobes a little larger and stouter than dorsal lobes; all the lobes broadly margined with dark brown, these marks expanding at inner ends; on ventral lobes, lateral margin expanded at inner

end and continued across disk, meeting its fellow of the opposite side between spiracles; dorsal margin of lateral lobes touching spiracles; each of the lobes marked with a capillary dark brown line down center of inner face, this beginning near ends of lobes and extending almost to base; lobes fringed with long hairs, these very tiny near base, longer near tips of lobes, but scarcely, if at all, interrupted between lobes. Spiracles large, circular, separated by a distance a little greater than diameter of one. Anal gills six, long, slender, unbranched.

Head capsule of the usual tipuline type. Labrum covered with dense, short hairs, those on lateral lobes longer. Mentum (Plate XCI, 498) usually seven-toothed, in some cases nine-toothed; median tooth slender, lateral teeth flattened, subacute. Hypopharynx (Plate XCI, 499) narrow, five-toothed. Antenna (Plate XCI, 500) long and slender; first segment a little enlarged near base; at apex several tiny sensory papillae; auditory plate near base of segment. Mandible (Plate XCI, 501) moderately large, with two large dorsal and about three ventral teeth; prostheca large. Maxilla small; palpus large, cylindrical, apex truncated.

Pupa.— Length, 15–22 mm.
Width, d.-s., 2.4 mm.
Depth, d.-v., 2.6 mm.

Coloration dark brown; lateral and posterior margins of abdominal segments paler. (In old specimens the general coloration is very dark brown; in younger specimens the abdomen is more or less distinctly lined with brown.)

Thorax subterete; abdomen depressed, lateral margins flattened. Labrum broad, apical point narrow. Labial lobes broad, slightly separated on median line. Maxillary palpi short, stout, apex recurved. Antenna moderately elongated, extreme tip darkened. Pronotal breathing horns long and slender, unequal in length, the longer about 9 or 10 mm. in length, the other 6 mm., at tips split into divergent flaps (Plate XCI, 504) almost as in the hexatomine genera Pseudolimnophila and Pilaria, which live in the same muddy situations. Mesonotum (Plate XCI, 503) transversely wrinkled. Leg sheaths reaching posterior margin of third abdominal segment; hind legs the longest; middle legs a little shorter than fore legs.

Abdominal segments divided into a basal and a posterior ring; tergites with basal ring unarmed; posterior ring with a subterminal transverse row of short spines, with a few setae located on lateral face of some of the spines; on second tergite, four to six spines, on tergites 3 to 7, three to fifteen spines; two small spines with setae near anterior lateral angle of posterior ring; pleurites with a small setiferous spine on basal ring, and two such spines on posterior ring located side by side; sternites with the basal ring unarmed, posterior ring armed similarly to that of tergites; in addition to posterior row of spines, a pale oval area on either side of midventral line, each with two transversely placed spines. Male cauda (Plate XCI, 505) with four powerful lobes on dorsum of last segment, directed dorsad and slightly caudad, lobes bearing three or four small spines before tips; between anterior pair of lobes, two additional slender lobes, each ending in two acute spines.

Nepionotype.— Ringwood Hollow, Ithaca, New York, July 20, 1916.
Neanotype.— Cast pupal skin, type locality, November 20, 1916.
Paratypes.— Larvae and pupal skins, type locality.

Genus **Tipula** Linnaeus (Lat. *a water-strider*)

1758 *Tipula* Linn. Syst. Natur., ed. 10, p. 585.
1842 *Pterelachisus* Rond. Mag. Zool. Ins., pl. 106.
1864 *Anomaloptera* Lioy. Atti dell' Institut Veneto, ser. 3, vol. 9, p. 218.
1887 *Oreomyza* Pokorny. Wien. Ent. Ztg., vol. 6, p. 50.
1894 *Manapsis* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 222.
1894 *Rhadinobrochus* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 223.
1894 *Tipulidea* Scudder. Proc. Amer. Philos. Soc., vol. 32, p. 238–239.
1916 *Nippotipula* Mats. Thous. Ins. Japan, add. 2, p. 457–458.
1916 *Platytipula* Mats. Thous. Ins. Japan, add. 2, p. 459.
1916 *Yamatotipula* Mats. Thous. Ins. Japan, add. 2, p. 461–462.
1916 *Togotipula* Mats. Thous. Ins. Japan, add. 2, p. 465.

Larva.— Form generally stout, terete or nearly so. Integument with pubescence and almost invariably with a definite chaetotaxy. Spiracular disk surrounded by six or rarely eight lobes, simple, or in certain species (as *T. abdominalis*) more or less split at their tips. Spiracles small and widely separated (in *T. abdominalis*), or in other species large and rather close together. Anal gills almost invariably present, with six or eight branches, these branches simple, not pinnate. Head capsule compact and massive. Labrum broadly transverse. Mandible usually small, with few teeth, ventral cutting edge with usually two or three teeth. Maxilla rather complicated, of the generalized tipuline structure. Antenna usually elongated, basal segment two to four times as long as it is thick, stouter in species living in decaying wood. Mentum with seven to nine teeth. Hypopharynx a flattened plate, anterior margin usually with five teeth.

Pupa.— Form generally stout. Cephalic crest lacking or very small, with rudimentary setae. Mouth parts as in the subfamily, sheaths of maxillary palpi strongly recurved at tips. Pronotal breathing horns subequal in length, short, stout, usually straight, tips but little expanded. Mesonotum transversely wrinkled, in some wood-inhabiting species (as *T. trivittata*) with about four conspicuous tubercles. Wing sheaths and leg sheaths moderate in length. Abdominal armature usually strong, each segment with a posterior row of four to twenty spines; in some species a basal ventral row of spines on posterior ring of segments. Cauda with dorsal armature of four powerful lobes; eighth segment adding, as a rule, ten spines, of which six are ventral and lateral in position, and two or four are dorsal; dorso-median pair lying between anterior pair of lobes of cauda, as discussed above, and lacking or very reduced in some wood-inhabiting species (*T. trivittata*). Lateral abdominal spiracles lacking or merely vestigial.

Tipula is the largest genus of crane-flies, comprising a vast assemblage of species (between six and seven hundred described forms) which are found on all the continental areas of the world but are few in the Australasian region and apparently lacking on many of the lesser oceanic islands. The genus is one of extreme interest, and its study will require many years of conscientious application. Subapterous species are not rare in this group, of which many are far northern forms, others are coastal species, while a few live inland and under influences that make it difficult to explain their subapterous condition.

The immature stages of the various species are diverse in their habits, ranging from species that are nearly if not quite aquatic, thru the majority of the known forms which live in generally moist earth or mud along the margins of water bodies, to still others that live in the semi-decayed wood of prostrate tree trunks. Mellor (1919:64) has recorded Tipula larvae as breeding in manure. So far as is known, the larvae are herbivorous, tho they will eat animal food under stress (as described by Patterson [1908] for *Tipula oleracea*, which feeds in considerable numbers on earthworms).

In Europe, a great number of life histories in this genus have been worked out in commendable detail, mainly thru the efforts of Beling, who discusses no fewer than thirty species. His descriptions give a clear idea of the range in structure and habitat to be expected in the genus. The number of lobes surrounding the spiracular disk varies from four (apparently) in *T. selene* and related forms, to as many as eight in *T. subnodicornis*. Practically all of the known species show the normal tipuline number of lobes, six.

A summary of the larval habitats of the Palaearctic species is as follows:

1. Species living in saturated earth along watercourses or in débris at the water's edge, or species that are aquatic — *Tipula fulvipennis* de Geer, *lateralis* Meig., *lunata* Linn., *maxima* Poda, *variicornis* Schum., *variipennis* Meig., *vittata* Meig.
2. Species living in earth, usually in woods, underneath a mold of leaves or coniferous needles — *Tipula caesia* Schum., *dilatata* Schum., *fulvipennis* de Geer, *hortensis* Meig., *hortulana* Meig., *nigra* Linn., *nubeculosa* Meig., *ochracea* Meig., *pabulina* Meig., *paludosa* Meig., *pruinosa* Wied., *scripta* Meig., *selene* Meig., *truncorum* Meig., *unca* Wied., *variipennis* Meig., *vittata* Meig.
3. Species living in earth in gardens, pastures, or meadows, usually beneath turf — *Tipula irrorata* Macq., *luteipennis* Meig., *nigra* Linn., *ochracea* Meig., *oleracea* Linn., *paludosa* Meig., *pruinosa* Wied., *subnodicornis* Zett., *truncorum* Meig., *vernalis* Meig.
4. Species living in or beneath cushions of moss or in earth overgrown with a mossy covering — *Tipula dilatata* Schum., *hortulana* Meig., *marmorata* Meig., *pagana* Meig., *peliostigma* Schum., *pruinosa* Wied., *rufina* Meig., *signata* Staeg., *truncorum* Meig., *unca* Wied.
5. Species living underneath moss on logs — *Tipula irrorata* Macq.
6. Species living in decaying wood — *Tipula flavolineata* Meig., *irrorata* Macq., *truncorum* Meig.

Bouché describes *T. lunata* and *T. ochracea* as living in decaying willow wood, and Sopotzko records *T. flavolineata* as injuring clover; but these records are presumably based on mistaken identifications.

Comparatively few of the eastern American species have been reared, and it is not considered advisable to attempt a key to the larvae or the pupae at this stage of knowledge of the subject. Such a key would

include but a fraction of the possible species and would be of little value. It will require the careful rearing of species for many years before a workable key to the immature stages of the eastern species of the genus can be produced. The characters that will prove of greatest value in the separation of the larvae and the pupae of the species of Tipula are as follows:

Larvae

1. *Anal gills.* (These are rarely lacking, and the number and arrangement of the branches, their form, and their function, are of primary importance.)
2. *Spiracular disk.* Number of lobes surrounding disk and whether they are simple or branched; character and nature of fringe of hairs around disk, if such is present; size, shape, and distance apart of spiracles; markings on inner face of disk and lobes.
3. *Chaetotaxy.* Arrangement, length, and number of setae on segments.
4. *Body form.* Terete, subdepressed, or flattened ventrally only; clothing of pubescence, and pattern formed on dorsum.
5. *Head capsule.* (The head is remarkably uniform thruout the group, a condition to be expected in a group so compact as Tipula.) Shape of mentum and hypopharynx, and number, size, and shape of teeth along their anterior margins; shape of antenna, and other details of head.

Pupae

1. General form, whether terete or depressed.
2. Mouth parts.
3. Pronotal breathing horns, their relative length, size, and form.
4. Armature of mesonotum.
5. Wing sheaths and leg sheaths.
6. Spines on abdominal segments, their size and number; whether lacking or present at base of posterior ring of sternites; arrangement and number of pleural spines.
7. Cauda, shape of genital sheaths, armature of dorsum, and ventral margin of eighth sternite.

Descriptions are given in the following pages of about ten life histories which are entirely new or have been insufficiently considered elsewhere. A few notes on certain other species that have been observed in the past few years may be added here:

Tipula cayuga Alex. A conspicuous yellow larva, living in organic earth beneath leaves, in association with *Bittacomorphella jonesi* and other forms which are discussed elsewhere (page 781). The pupal duration is slightly over seven days.

T. angustipennis Loew. Found living in rather dry earth beneath leaves in shaded woods (Lawrence, Kansas, Mrs. C. P. Alexander).

T. umbrosa Loew. Occurs in garden soil in company with the larvae of *Tipula bicornis* Forbes.

T. fuliginosa Say. Reared from larvae living in débris under the nest of a turkey vulture (Jackson Island, Maryland, May 23, 1913, R. C. Shannon).

T. sayi Alex. and *T. tricolor* Fabr. In saturated mud in marshy or swampy situations.

T. tephrocephala Loew. A large larva, nearly if not quite aquatic in its habits.

The life histories of other Nearctic species are recorded in the summary of literature on page 980. These are as follows: *Tipula arctica* Curt. (Nielsen, Alexander), *T. eluta* Loew (Hart, Malloch), *T. cunctans* Say (Hyslop, Malloch), *T. bicornis* Forbes (Forbes), and *T. ultima* Alex. (Needham, Caudell). *T. arctica*, according to Nielsen (1910:57–59), was found commonly in eastern Greenland. The immature stages were discovered in circular holes from two to three centimeters deep in the ground, especially beneath tufts of *Cassiope tetragona* (L.) D. Don. The pupae were found at the end of June, and empty pupa cases were found as early as the 25th of the same month. According to Nielsen, the larvae require two years to attain their growth.

Tipula (Trichotipula) oropezoides Johns.

1909 *Tipula oropezoides* Johns. Proc. Boston Soc. Nat. Hist., vol. 34, p. 131–132.

Larvae of *Tipula oropezoides* were first found on March 30, 1917, living beneath saturated moss in Needham's Glen, Ithaca, New York, where they were associated with larvae of *Dicranomyia badia*, *Penthoptera albitarsis*, *Tipula collaris*, and other species. Numerous additional larvae were found in the same locality on April 18, 1917. Some of these were placed in rearing and emerged on May 6. The larvae are nocturnal in their habits, being very sluggish and retiring during the day but becoming active after sunset.

The adult flies bear a strong resemblance to species of the genus Oropeza, with which they are sometimes found associated. They may often be swept from rank herbage in cool Canadian woods.

Larva.— Length, 16.5–17 mm.
Diameter, 1.8–2 mm.

Coloration above, a deep velvety brown with mottlings of paler; on basal ring of tergites six median transverse pale spots, posterior ring less regularly marked; pleura and venter pale. (The dark markings on the dorsum are produced by patches of dark-colored hairs, which cover the body densely in places.)

Form subterete. Integument with an abundant pubescence, longest on dorsum. Chaetotaxy as follows: dorsum (Plate XCIII, 516) on posterior ring with six stout setae, three on either side, the middle seta a little closer to the inner seta; ventral segments (Plate XCIII, 517) with four setae, two anterior and two posterior, the latter a little more separated. Spiracular disk (Plate XCIII, 518) surrounded by six approximately subequal lobes, their inner faces heavily lined with dark brown; at tip of each lobe a pale rounded spot, largest on ventral lobes and here with a sensory bristle; lateral mark not reaching spiracles; lateral and dorsal lobes slightly paler medially; above and below each spiracle a transverse brown

line; on disk, between spiracles, two indistinct dusky spots; lobes fringed with rather short, pale hairs which are narrowly interrupted between lobes. Spiracles irregular, roughly triangular. Anal gills four, slender, posterior pair the larger (Plate XCII, 506).

Head capsule as in genus. Labrum and maxilla very densely fringed with long golden-yellow hairs. Mentum (Plate XCIII, 513) with two flattened lateral teeth, the median point elongated; mentum very deeply split behind. Hypopharynx (Plate XCIII, 514) with but three evident teeth, the lateral teeth very broad, flattened. (In some specimens these teeth are all very blunt, so that the anterior margin of the hypopharynx appears merely crenulate.) Antenna with apical disk very flattened. Mandible (Plate XCIII, 515) with a dorsal tooth and a powerful ventral tooth.

Pupa.— Length: male, 12 mm.; female, 12.5–13 mm.
Width, d.-s.: male, 1.6–1.7 mm.; female, 1.8–1.9 mm.
Depth, d.-v.: male, 1.6 mm.; female, 1.7–1.8 mm.

Coloration dark brown; dorsum of thorax and abdomen, and face, more reddish brown. General features as in *Tipula collaris.* Form slender. Pronotal breathing horns long and slender, dark-colored, divergent at tips. Antenna elongate. Wing sheaths ending opposite apex of second abdominal segment. Leg sheaths long, extending to beyond mid-length of fourth abdominal segment. Male cauda with dorsal lobes of genitalia short, blunt; ventral lobes produced caudad into slender, blunt lobes which are transversely wrinkled, separated by a U-shaped notch, at base on outside with a prominent spine. Female ovipositor elongate; dorsal valves narrowed to the blunt tip; ventral lobes stout, a little shorter than dorsal valves, tips strongly divergent; the six dorsal lobes of cauda spinous-tipped, sharply pointed.

Nepionotype.— Ithaca, New York, April 18, 1917. No. 6–1917.
Neanotype.— With type. No. 7–1917.
Paratypes.— Numerous larvae and pupae.

Tipula collaris Say

1823 *Tipula collaris* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 23.

Larvae and pupae of *Tipula collaris*, a common vernal crane-fly, occurred frequently beneath saturated moss (*Amblystegium irriguum* [Wils.] B. & S.) in Needham's Glen, Ithaca, New York, on April 17, 1917. Their associates are noted under the account of *T. oropezoides* (page 1001). In the same moss areas occurred numerous small red-backed salamanders (*Plethedon cinereus*), which probably fed on the insect denizens of the place. Specimens emerged in the writer's breeding jars as late as May 10.

The adults are on the wing during April and May, some persisting into early June in cool northern woods. The life history undoubtedly requires a year for its completion.

Larva.— Length, 21.5–25 mm.
Diameter, 2.5–3.5 mm.

Coloration pale dusky, darker above; dorsum behind with two broken lines which are divergent on each annulus, those of anterior annulus made up of three circular spots; pleura with a conspicuous dark brown stripe; venter almost uniformly pale, with indistinct lines; anterior part of thoracic segments darker. (In life the color is rich reddish brown, and the pleural stripe is not evident.)

Form terete. Body covered with a delicate, pale pubescence, in addition to the usual setae. Chaetotaxy as follows: tergites (Plate XCIV, 521) with a transverse row of six setae on posterior ring before margin, the two innermost solitary, each lateral pair closely approximated; a solitary seta on extreme lateral margins of tergite, at margin of dark pleural stripe, and at about midlength of posterior ring; pleura on basal ring with a single seta, posterior ring with a group of about three or four setae, one larger than the others; sternites with four widely separated setae on posterior ring, the lateral pair a little nearer posterior margin than the median pair. Spiracular disk (Plate XCIV, 522) surrounded by six lobes which are moderately slender; ventral pair a little longer, dorsal pair a little shorter; all the lobes broadly margined with pale brown; ventral lobes having in addition a black capillary line extending from tips backward to beyond midlength of lobes, this line broadest at tip, gradually narrowing, and becoming paler toward base of lobes; below each spiracle, two conspicuous black dots; lobes fringed with numerous rather long hairs. Spiracles large, separated by a distance a little greater than diameter of one. Anal gills six, one pair much shorter than the others, consisting of a basal branch of the anterior gill.

Head capsule rather small, of the usual tipuline type. Mentum (Plate XCIV, 519) very broad, anterior margin almost transverse, seven-toothed, median point the longest. Hypopharynx (Plate XCIV, 520) with five teeth, which are very short and blunt giving anterior margin a deeply crenulated appearance; before hypopharynx a rounded lobe which is densely covered with six short, blunt, chitinized points, this being probably the prementum. Antenna elongate-cylindrical; apex with apical disk very small, button-like. Mandible small, with about one dorsal and two ventral teeth. Maxilla slender, densely hairy; palpus subglobular, with several small, hyaline papillae.

Pupa.— Length, 17–19 mm.
Width, d.-s., 2.8–3.2 mm.
Depth, d.-v., 3–3.3 mm.

Coloration brown; wing sheaths, except in older individuals, pale; pleural region of abdomen light yellow; abdominal incisures often pale.

Head rather small. Cephalic crest low and indistinct, with tiny setae. Labrum broad, apex pointed. Labial lobes oval, contiguous at inner end. Maxillary palpi strongly recurved at tips. Antenna slender, moderately elongated, extending some distance beyond wing root. Pronotal breathing horns equal in length, rather short, the moderately long tips flattened, smooth; two small, approximated setae on either side of median line. Wing sheath (Plate XCIV, 523) extending just beyond end of second abdominal segment; venation distinct. Leg sheaths extending beyond base of fourth abdominal segment; fore tarsi considerably shorter than the others.

Abdominal segments with armature of posterior ring weak, the spines very short and stout, with a few setae; maximum number of spines on the tergites about twenty; lateral anterior angle of posterior ring of tergites with two small spines; pleurites with one basal spine, and

three setiferous spines on posterior ring, arranged transversely; spiracles very rudimentary, opposite base of posterior ring; sternites with spines slightly more numerous and stouter; near base of posterior ring two transverse spines on either side median line, the outermost setiferous. Male cauda on dorsum with six lobes; the four posterior ones stout, with tips spinous or those of ventral pair slightly bifid; the two anterior median lobes shorter and more slender; eighth sternite with four large spines about equally spaced; eighth pleurite with a large, powerful, acutely tipped lobe, and two or three smaller dorso-lateral spines above base of middle pair of dorsal lobes. Female cauda almost the same as male cauda, due to the blunt terebral sheaths of this species.

Nepionotype.— Ithaca, New York, March 30, 1917.
Neanotype.— With type larva.
Paratypes.— Numerous larvae and pupae, March 30 to April 18, 1917.

Tipula nobilis (Loew)

1864 *Pachyrrhina nobilis* Loew. Berl. Ent. Ztschr., vol. 8, p. 62.

Larvae of *Tipula nobilis* were found in wet moss and beneath decaying witch-hazel leaves at Orono, Maine, on June 17, 1913. An adult emerged on July 1. A fully grown pupa found on July 11 attempted to transform, but died after two hours without being able to extricate itself from the pupal case.

The adults, which strikingly resemble some species of Nephrotoma, fly somewhat later than does *T. collaris*, but both species may be taken together in early June.

T. nobilis is very similar in all respects to *T. collaris*.

Larva.— Length, 20 mm.
Diameter, 2.9–3 mm.

Coloration, reddish brown.

Spiracular disk as in *T. collaris*, the brown lateral margin to the lobes a little paler. Anal gills as shown in Plate XCII, 507.

Head capsule almost as in *T. collaris*. Mentum with apical point elongate, with three blunt teeth on either side. Hypopharynx with five moderately acute teeth. Antenna with a blunt conical papilla, larger and more conspicuous than in *T collaris*. Mandible with teeth very blunt.

Pupa.— Length of cast pupal skin, about 18.5 mm.

Pupa very similar to that of *T. collaris*.

Nepionotype.— Orono, Maine, June 19, 1913. No. 40-1913.
Neanotype.— With type.

Tipula bella Loew

1863 *Tipula bella* Loew. Berl. Ent. Ztschr., vol. 7, p. 291–292.

Tipula bella is a common species, flying thruout the summer. Larvae and pupae are not rare in sandy or loamy soil along streams. A larva taken on April 28, 1917, in gravel at Ithaca, New York, where it was associated with larvae of Hexatoma, was placed in rearing. It emerged as an adult male on May 15. On May 27, 1913, three fully colored pupae were found along the sandy banks of Fall Creek, Ithaca, in association with *Eriocera spinosa*. They emerged as females on May 29 and 30.

Larva.— (The description is from field notes on the larva mentioned above.)

Length, 20–25 mm.

Coloration light grayish brown, with a slight reddish cast most noticeable on venter; dorsum with two narrow, almost continuous, dark brown lines, these lines subparallel at anterior part of each segment, then strongly bellied out, and then parallel but finally divergent.

Spiracular disk surrounded by six rather short lobes; ventral lobes with a linear, rather pale, brown mark, and a few sensory bristles at tips; lateral lobes with ventral margin lined with brown; dorsal lobes with both margins feebly bordered with brown; two small brown dots below each spiracle. Anal gills six, very long and slender.

Pupa.— Length of cast pupal skin, about 24 mm.

Pupa similar to pupae of other species of genus. Pronotal breathing horns short, cylindrical, narrowed to tips. Spines on abdominal segments rather large, especially on sternites; spines on base of posterior ring of sternites small but evident. Female cauda with dorsal valves long, pointed; sternal valves shorter. Cauda with the usual six lobes on dorsum, the four posterior stout, divergent, spinous-tipped, the anterior median pair much smaller; venter of segment 8 with three strong spines on either side, gradually smaller from lateral spine toward innermost spine.

Neanotype.— Ithaca, New York, reared May 25, 1917.
Paratypes.— Pupal skins, type locality, May 5, 1914 (No. 42-1914); August, 1911; May 25, 1917; etc.

Tipula caloptera Loew

1863 *Tipula caloptera* Loew. Berl. Ent. Ztschr., vol. 7, p. 292.

The vigorous larva of *Tipula caloptera* is one of the largest and most striking in the family. The larvae live in rapid- or slow-flowing streams either in the water among débris and under stones, or in the sand, gravel, or mud in very close proximity to the water. Here they are associated with the larvae of various species of Eriocera, *Erioptera armata*, Tabanus, Atherix, and other forms. Oftentimes they are found in deep water in exceedingly lotic situations. A larva placed in rearing on April 19, 1917, emerged as an adult female on May 13.

This is evidently the larva taken by Dr. Needham in the Adirondacks and referred by him with some doubt (Needham and Betten, 1901:575–576) to *T. abdominalis*. This dubious reference has created considerable confusion ever since the species was figured on the cover of *Entomological News* under the facetious name "*Quisnam sexcaudatus?*" Malloch (1915–17b:200–201) mentions the same larva under the name *T. abdominalis*. As stated elsewhere, the larva of *abdominalis* is very different.

Larva.— Length, 45–55 mm.
Diameter, 4.8–6.8 mm.

Coloration above, dark brown or brownish green; segments beautifully marked with small white spots, especially anterior segments; a broad, dark brown, median stripe, and a more or less distinct pale lateral stripe (in preserved specimens the pleura is usually dark brown, more distinct behind, with numerous pale white dots); sternum dark greenish. (In older specimens the color is very dark and the pattern is more or less obliterated.)

Form stout, terete. Body smooth, segments with indistinct posterior tubercles. Chaetotaxy very weak, a few weak pleural setae on posterior ring, sternal and tergal setae minute. Spiracular disk rather small, surrounded by six subequal, moderately narrow, lobes which are fringed with short hairs; margins of disk and lobes somewhat as in *T. bella*, each lobe with a delicate capillary brown line; two brown spots beneath each spiracle. Spiracles small, separated by a distance about equal to twice diameter of one. Anal gills six, very long and slender (Plate XCII, 508).

Head capsule as in genus. Mentum broad; anterior margin nearly transverse, with three subacute teeth on either side, median point not conspicuously elongated.

Pupa.— Length of cast skin, about 32–35 mm.

Characters almost as in *T. bella*. Pronotal breathing horns short, cylindrical, tips not expanded. Abdominal spines prominent, projecting, few in number, on intermediate tergites 9 or 10; pleurites with a single strong spine on each ring; sternites with a posterior row of seven or eight strong spines; on segments 5 to 7 two strong spines at base of posterior ring, those of seventh segment the largest. Cauda almost as in *T. bella*.

Nepionotype.— Ithaca, New York, April 26, 1917. No. 16–1917.
Neanotype.— Cast pupal skin, reared May 13, 1917.
Paratypes.— Larvae and cast pupal skins from type locality.

Tipula dejecta Walk.

1856 *Tipula dejecta* Walk. Ins. Saunders, vol. 1, Dipt., p. 442.
1901 *Tipula fumosa* Doane. Journ. N. Y. Ent. Soc., vol. 9, p. 99.

Tipula dejecta is a characteristic vernal species flying in April and May. The flies are notable inhabitants of swamps, especially alder swamps.

On April 20, 1917, the writer found larvae of this fly in Larch Meadows, near Ithaca, New York, in association with larvae of *Rhamphidia mainensis*, *Pseudolimnophila luteipennis*, and other swamp inhabitants. The

conditions are discussed more fully under the account of Rhamphidia (page 831). The larvae are reddish brown in color, and rather sluggish. One of the larvae found on April 20 pupated on the 22d and emerged as an adult female on the 30th, a pupal duration of eight days. An additional pupa was taken, associated with larva of *Pseudolimnophila luteipennis*, *P. inornata*, *Tricyphona inconstans*, and other species.

Larva.— Length, 20 mm.
Diameter, 1.8 mm.

Coloration brown; dorsum marked with light and dark brown; a narrow, indistinct, dark brown, median line, with a broader zigzag brown line on either side; ventral surface a little paler.

Body covered with a short, dark pubescence at sides of segments, at margins longer and more conspicuous. Chaetotaxy as follows: tergites with six strong setae in transverse alinement, the outermost in pairs; two strong setae on each pleural annulus; posterior ring of sternites with eight strong setae, arranged in four pairs. Spiracular disk (Plate XCV, 526) pale, surrounded by six approximately equal lobes which are heavily marked with brown; dorsal and lateral pairs pointed, ventral pair blunt; ventral lobes with apical half shiny black, on ventral inner margin continued dorsad, almost contiguous on midline; inner face of dorsal and lateral lobes suffused with dark brown, proximal margin of dorsal lobe produced inward so that the marks are almost contiguous on median line; beneath each spiracle a transversely rectangular, dark brown mark. Anal gills with four anterior lobes which are long and slender, and a pair of rudimentary blunt posterior gills (Plate XCII, 509).

Head capsule and mouth parts as in genus. Mentum (Plate XCV, 524) seven-toothed, apical point the longest. Hypopharynx (Plate XCV, 525) bluntly five-toothed.

Pupa.— Length, 15.3 mm.
Width, d.-s., 2.3–2.4 mm.
Depth, d.-v., 2.1–2.2 mm.

Coloration dark brown; abdominal incisures paler.

Form relatively stout. General features as in genus. Cephalic crest consisting of two blunt lobes with microscopic setae. Maxillary palpi strongly curved at tip, but not entirely recurved. Pronotal breathing horns short, tips a little enlarged.

Abdominal tergites with spines weak, on median area of each row weak or lacking; on intermediate segments about fifteen spines; pleurites with only a single weak spine on basal ring; on posterior ring a rudimentary anterior spine and a somewhat larger posterior spine; sternites similarly armed to tergites, but spines fewer in number and larger, on segment 5 about twelve in number; on base of posterior ring a large spine on either side median line and a small setiferous tubercle laterad of each. Female cauda with tergal valves of ovipositor long and straight, sternal valves a little shorter; cauda with the usual six dorsal lobes, these terminating in slender spines; at end of eighth sternite six large spines; dorsal spines reduced to a single small pair, one near each lateral margin.

Nepionotype.— Larch Meadows, Ithaca, New York, April 20, 1917.
Neanotype.— With type.
Paratypes.— Two pupae with type pupa.

Tipula usitata Doane

1901 *Tipula usitata* Doane. Journ. N. Y. Ent. Soc., vol. 9, p. 124.

A large number of fully grown larvae of an unknown species of Tipula were found beneath the bark of a fallen tree at Stanford University, California, on March 22, 1915, by Harold Morrison. They were sent to the writer at Ithaca, New York, and emerged as adults on April 15. The immature stages are very distinct, closest perhaps to *T. trivittata*, which also lives beneath the bark of decaying trees. Nothing is known of the habits of the adult flies.

Larva.— Length, 25–27 mm.
Diameter, 3–3.2 mm.

Coloration pale greenish yellow, darker above.

Form terete. Body with a very sparse pubescence. Chaetotaxy as follows: tergites (Plate XCV, 527) with a posterior row of eight setae, the middle pair of each side very closely approximated; a seta near lateral margin at base of posterior ring, on a level with pleural seta; pleurites, one seta on each ring; sternites with eight setae in closely approximated pairs on posterior ring. Spiracular disk (Plate XCV, 528) surrounded by six lobes; dorsal and lateral pairs slender, tips of former acute; ventral lobes blunt; ventral lobes with tips blackened, continued down proximal margin of lobes as a paler brown line; lateral lobes with inner face narrowly blackened, this mark not reaching spiracles; dorsal lobes with entire inner face bulging, intensely black, the marks contiguous at their basal inner angle; an indistinct brown spot underneath each spiracle, in some specimens this mark continuous with that of ventral lobes; lobes not fringed with hairs. Spiracles large, separated by a distance about equal to, or a little greater than, diameter of one. Anal gills short and blunt, strongly protuberant, surrounding anus as four fleshy lobes (Plate XCII, 510).

Head capsule as in genus. Mentum broad, with seven to nine teeth, in the latter case the outermost pair very small. Hypopharynx with three or five very blunt teeth. Antenna much shorter and stouter than in most species of Tipula, the length only a little greater than twice the diameter, at apex with a blunt conical papilla and a few small, cylindrical sense pegs. Mandible powerful, with two or three flattened teeth on ventral cutting edge.

Pupa.— Length, 15–16.8 mm.
Width, d.-s., 2 mm.
Depth, d.-v., 2.3–2.4 mm.

Coloration pale brown; posterior margin of abdominal rings pale; lateral margin of abdomen conspicuously pale yellowish white.

Form slender. Pronotal breathing horns narrow, a little expanded at tips. Leg sheaths ending on a level.

Abdominal spines very strong, but few in number; tergites with four to six spines; pleurites with a single weak spine on each ring; sternal spines very strong, five or six in number, those on segment 7 subequal in size to those on segment 8; no sternal spines on base of posterior ring. Male cauda with posterior dorsal lobe very strong, pale, tips acute; lateral lobes greatly

reduced in size, the median pair represented only by two blunt brown tubercles; eighth segment with the usual six strong ventral and lateral lobes. Female ovipositor with valves small; sternal valves short and broad, much shorter than tergal valves.

Nepionotype.— Stanford University, California, April 15, 1915.
Neanotype.— With type, bred April 15, 1915.
Paratypes.— Numerous larvae and pupae with type.

Tipula trivittata Say

1823 *Tipula trivittata* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 26.

The larvae and the pupae of *Tipula trivittata* live beneath the bark of much-decayed prostrate trunks or under the layers of moss that often cover fallen trees. Abundant larvae were found on March 22, 1913, and were placed in rearing, adults emerging on April 26. On April 16, 1914, larvae of two distinct sizes — some very small and some nearly fully grown — occurred in abundance beneath moss (*Entodon seductrix* [Hedw.] C. Muell., *Brachythecium acuminatum* [Hedw.] Kindb., *Hypnum Haldanianum* Grev., and *Mnium sylvaticum* Lindb.) on prostrate decaying elms, sycamores, and other trees, at Renwick Park, Ithaca, New York.

The adult flies are among the commonest of the eastern species of Tipula, and fly during a large part of the season.

Larva.— Length, 24–25 mm.
Diameter, 2.7–3 mm.

Coloration pale brownish yellow, a little paler beneath.

Form moderately elongated, terete. Pubescence very short or practically lacking. Setae on anterior segments strong, on posterior segments shorter. Chaetotaxy as follows: tergites with a posterior row of six setae, the two middle punctures each with a single seta, the two lateral punctures each with two setae; pleurites with a single seta on each ring; sternites with two rows of setae, the anterior row consisting of two closely approximated groups of two setae each, the posterior row consisting of a single large seta, laterad of which is a minute bristle. Spiracular disk (Plate XCV, 529) surrounded by six lobes; lateral pair long and slender; dorsal pair a little shorter, slender; ventral lobes blunt; ventral lobes with a jet-black mark on inner face; lateral lobes with dark markings represented only by a very small linear dash; dorsal lobes with a small black area. Spiracles large, separated by a distance a little less than diameter of one. Anal gills indistinctly lobed, four in number, two on either side, very blunt and protuberant.

Head capsule as in genus, the mouth parts almost as in *T. usitata*. Mentum broad, with seven teeth. Hypopharynx with five teeth, the three middle ones the longest, subequal in size. Antenna shorter and stouter than is usual in the genus.

Pupa.— Length, 19–20 mm.
Width, d.-s., 2.5–2.6 mm.
Depth, d.-v., 2.8–3 mm.

Coloration dark brown; abdomen yellow, with a broad sublateral brown stripe on both sternites and tergites; abdominal segments beyond posterior row of spines brighter, more yellowish.

Characters of head as in genus. Cephalic crest very small. Labrum broad. Pronotal breathing horns short, slightly curved. Mesonotal prescutum with fine transverse wrinkles; two blunt lateral tubercles, and behind these, on either side of median line, two smaller flattened ledges which are often bifid at their tips. (Similar ledges, but much less prominent, occur in *T. usitata.*)

Abdominal tergites with subapical armature weak, spines varying in number from six to eight, those of posterior segments larger; pleural spines long and slender, one on each ring; sternal spines powerful, four to six in number, no spines on base of posterior ring. Female cauda with sternal valves long and slender, but little shorter than tergal valves; dorsal lobes of cauda four in number, posterior pair very powerful, lateral pair small, anterior median pair lacking.

Nepionotype.— Ithaca, New York, March 22, 1913.
Neanotype.— With type.
Paratypes.— Numerous larvae and pupae with types, April 26, 1917; March 22, 1913; etc.

Tipula ignobilis Loew

1863 *Tipula ignobilis* Loew. Berl. Ent. Ztschr., vol. 7, p. 280.

The adult flies of *Tipula ignobilis* are not common in collections, due in part to their retiring habits. The larvae, however, are common in their preferred habitat, saturated moss cushions.

At Orono, Maine, numerous larvae were taken in wet moss on June 17, 1913, associated with other larvae, such as those of Rhaphidolabina, Tricyphona, Pedicia, and *Tipula nobilis*. At Ithaca, New York, on April 23, 1917, four very small larvae were found in wet cushions of moss (Amblystegium). They grew very rapidly, emerging as adults on May 21. On May 22 this moss was carefully examined and about thirty fully grown to rather immature larvae of this species were taken. They were associated with equally numerous larvae of *Dicranomyia stulta* O. S. At Needham's Glen, the species occurred in the same moss that earlier in the season harbored *Tipula collaris* and *T. oropezoides*. On June 14 two teneral adults of *T. ignobilis* were captured, in company with *Dicranomyia stulta*, *Geranomyia canadensis*, *Dactylolabis montana*, and other species. The species is very common at the Indian Ladder, Helderberg Mountains, New York.

Larva.— Length, 16.5–18 mm.
Diameter, 2.5–2.6 mm.

Coloration grayish brown, paler gray beneath; thoracic segments conspicuously reddish brown.

Body terete. Dorsum covered with a short, dark pubescence, which gives upper surface its dark color. Chaetotaxy as follows: tergites (Plate XCVI, 530) with a posterior transverse row of two setae near base of posterior ring; sternites (Plate XCVI, 531) with about eight setae, anterior median row consisting of two large setae, each with a tiny seta proximad of it, the posterior pair of large setae more widely separated, laterad of each of these two closely approximated smaller setae. Spiracular disk (Plate XCVI, 532) surrounded by six moderately long lobes fringed with rather short, pale hairs; tips of ventral lobes with a pale circular area provided with a sensory seta; inner face of spiracular disk with the markings pale, ventral lobes with an indistinct capillary brown line; two brown spots beneath each spiracle. Spiracles large. Anal gills eight, consisting of a transverse row of four short, slender, two-branched lobes (Plate XCII, 511).

Mentum of head capsule with median point prominent, the three lateral teeth of either side small, moderately acute. Mandible with about four teeth, in addition to the large basal prosthecal tooth.

Pupa.— Length: male, 12 mm.; female, 14–15 mm.
Width, d.-s.: male, 1.7–1.8 mm.; female, 1.8–2 mm.
Depth, d.-v.: male, 1.9–2 mm.; female, 2.1–2.2 mm.

Head and mouth parts as in genus. Pronotal breathing horns rather long and slender, tips a little expanded. Leg sheaths rather short, just exceeding third abdominal segment; hind legs a little the longest, the other tarsi ending about on a level.

Abdominal tergites with armature weak, spines small; pleurites and sternites with spines notably larger and more powerful; sternites with subterminal row consisting of twelve to fifteen spines, those of the sixth and seventh segments larger; no spines at base of posterior ring; pleural spines setiferous, very weak, one on basal ring, two on posterior ring. Male cauda with ventral lobes widely separated, terminating in slender, curved spines directed caudad; dorsal lobes slender, approximated on dorso-median line. Female cauda (Plate XCVI, 533) with tergal valves a little longer than sternal valves, the latter at their tips terminating in slender points directed ventrad and laterad; dorsum of cauda with the usual six lobes, posterior pair the largest, terminating in two distinct points; eighth segment on pleural and sternal region with six very powerful, curved spines.

Nepionotype.— Ithaca, New York, June 3, 1917.
Neanotype.— With larva, June 3, 1917.
Paratypes.— Numerous larvae and pupae, June 1 to 12, 1917.

Tipula abdominalis (Say)

1823 *Ctenophora abdominalis* Say. Journ. Acad. Nat. Sci. Phila., vol. 3, p. 18.

Tipula abdominalis is the largest eastern species of the genus, altho some specimens of *T. caloptera* are nearly as large. The adult flies are on the wing in late August and September, and even, in fewer numbers, in June and July.

The large, fleshy larvae occur beneath or among drift at or near the margins of streams. They are usually abundant under saturated decaying leaves or under tussocks of grass at the edge of the water. They are entirely herbivorous, feeding on diatoms, decaying plant tissues, and other vegetable matter. The larvae are readily distinguished from all other species of the genus by the small spiracles and the bifid or split lobes surrounding the spiracular disk. Pupation takes place in the mud or earth at the water's edge. Malloch's *Tipula* sp. 2 (1915–17 b: 200–201) seems to refer to *T. abdominalis*, but the mouth parts of his specimens do not seem to be normal.

Larva.— Length, 55–65 mm.
Diameter, 7.5–10 mm.

Coloration pale grayish brown; anterior end darker.

Form stout, terete, thin-skinned. Posterior ring of abdominal segment, both above and below, with a naked transverse welt, which bears the setae; this welt very protuberant at its lateral ends, almost like a pair of prolegs. Skin naked, except for a microscopic dotting and the rather short, delicate setae. Chaetotaxy as follows: tergites, on welt at about midlength, a transverse row of eight setae, the middle pair of each half closely approximated; pleurites with a single seta opposite basal ring, and two opposite posterior ring, arranged one behind the other; sternites with four pairs of setae on welts, anterior middle pair closer together than posterior lateral pair. Spiracular disk (Plate XCVII, 537) moderately large, flattened, truncated, surrounded by six deeply bifid and irregular lobes; ventral lobes elongate, with a blunt basal branch bearing two setae; posterior branch longer, indistinctly bifid at tip and with a few setae and several hairs; lateral lobes deeply bifid, the ventral one armed with lateral setae; dorsal lobes small, simple; inner faces of dorsal and lateral lobes with a narrow dark brown stripe, ventral lobes with two narrow, usually indistinct lines, these markings broadest and darkest on dorsal lobes. Spiracles very small, circular, separated by a distance about equal to four times diameter of one. Anal gills six, long and slender, the middle one on either side a little shorter than the others. Pleural region of penultimate segment of body with a blunt setiferous tubercle.

Head capsule and mouth parts about as in genus. Mentum (Plate XCVII, 536) broadly transverse, anterior margin with seven to nine teeth, in the latter case the outermost teeth very indistinctly separated from the sublateral teeth. Hypopharynx broad, anterior margin with teeth very indistinct.

Pupa.— Length of cast pupal skin, about 35 mm.

Pronotal breathing horns short, straight, cylindrical; apex short, and but little if at all expanded. Details of mouth parts as in other species of genus. Wing sheaths ending before apex of second abdominal segment. Leg sheaths extending to about opposite end of third abdominal segment; fore tarsi the shortest, hind tarsi the longest, ends of tarsal sheath thus forming a broad, inverted U-shaped notch.

Abdominal armature generally weak. Tergites (Plate XCVII, 538) with subterminal row broken, consisting of an anterior median pair of large spines, laterad of which are two or

three smaller spines; close to ends of row a bifid setiferous spine; pleurites with spines long, slender, directed strongly caudad, tips narrowly bifid, bearing a seta in notch; basal spine the largest; posterior spines two in number, anterior dorsal one the smaller; sternites (Plate XCVII, 539) with posterior row unbroken, of comparatively few spines, there being about eleven excluding the two larger spines at ends of row; the innermost of the large lateral spines conspicuously bifid, bearing a stout seta in its notch; base of posterior ring on either side of median line with a powerful conical spine which is acutely tipped. Female cauda as in genus, sternal valves conspicuously shorter than the long tergal valves; the six dorsal lobes powerful, chitinized, more or less bifid at tips; dorsal lateral lobes at end of eighth segment split before tips.

Nepionotype.— Cascadilla Creek, Ithaca, New York, May 31, 1913.
Neanotype.— Cast pupal skin, reared at Ithaca, September, 1911.
Paratypes.— Abundant larvae from type locality.

Tipula taughannock Alex.

1915 *Tipula taughannock* Alex. Proc. Acad. Nat. Sci. Phila., p. 476–479.

Tipula taughannock is of exceptional interest in the striking color dimorphism that it shows, the females being black and yellow, the males light yellowish. The following account of the habits of the adult flies is taken from the writer's field notes:

June 12, 1915. Deciduous forest association of the southern Helderberg Mountains, near the village of New Salem, Albany County, New York. This association is an open deciduous forest, with an undergrowth of Cystopteris, Geranium, Caulophyllum, and Impatiens. It is a very open woods, having an eastern exposure and with the talus slopes so old that an extensive vegetation has sprung up. The great boulders scattered about thru the woods have come from the high Silurian and Devonian cliffs above. The woods are of such a nature that much sunlight penetrates to the ground beneath. The forest cover shows a striking lack of coniferous species, but the following deciduous species are common: butternut, hop hornbeam, hard maple, basswood, white ash. The shrubbery consists of mountain maple, bladdernut, and a few dogwoods. The dominant herbage consists of jack-in-the-pulpit, wild ginger, bloodroot, bishop's-cap, false bishop's-cap, blue cohosh, white baneberry, herb robert, touch-me-not, waterleaf, bedstraw, and other characteristic flowering plants in fewer numbers, as well as several ferns, such as the bulbous bladder fern, maidenhair, and, on the rocks, the walking fern. The crane-fly under consideration is very common in these woods. The proportion of males to females is about one hundred to one, but this is due, in large part at least, to the very secretive habits of the latter. The males are untiring, almost always moving along, silently and relentlessly, in quest of their mates. They pass in and out among the dense herbage, usually close to the ground, occasionally fluttering up a tree trunk or over a mossy boulder which is covered with various bryophytes and walking ferns. They are so intent upon their quest that they are readily scooped up by hand. If this is attempted and fails, however, they become instantly alarmed and fly away with great speed, their flight at this time having a strong undulating motion. In a position of rest, the male almost always hangs on the under surface of a leaf, with the body directed straight toward the ground. Several specimens of this species, as well as of *Tipula trivittata* Say and *T. senega* Alex., were found dead in spider's webs. These small webs, made by species of Epeiridae and Linyphiidae, are very common on and between the leaves of herbaceous plants and are presumably intended for smaller game. The large Tipulas are probably taken in by accident.

The females are more active when in flight than are their mates and are capable of moving very rapidly. Their flight is a rapid, fluttering progression along the ground. Copulation takes place on either the upper or the lower surface of leaves, usually near the ground. Sometimes copulation is end to end, with the heads directed away from each other; at other times it is face to face, the bodies being arcuated into a convex loop.

The larva almost certainly lives among or beneath the decaying leaves and débris which cover the talus slope.

Tipula macrolabis Loew

1864 *Tipula macrolabis* Loew. Berl. Ent. Ztschr., vol. 8, p. 58.

Tipula macrolabis is distinctly northern in its distribution. It is a characteristic fly of northern deciduous woods in June. The following notes were made near the village of Indian Castle, Herkimer County, New York, on June 13, 1915:

A small woodland stream with a forest cover of trees such as hemlock, beech, slippery elm, and basswood, and a ground cover of false solomon's seal, wood nettle, wild ginger, herb robert, touch-me-not, waterleaf, sarsaparilla, and the two abundant ferns maidenhair and the bulbous bladder fern. The males of *T. macrolabis* were in search of the females, and fluttered up the tree trunks often to a height of ten or fifteen feet, flying close to the ground, around brush heaps, hovering about the leafy ends of branches, and performing similar actions in their untiring quest for their mates. They occurred in company with males of *T. fuliginosa* and *T. valida*, which were similarly engaged in searching for the females.

Tipuline No. 1 (possibly *Tipula iroquois* Alex.)

1863 *Tipula cincta* Loew. Berl. Ent. Ztschr., vol. 7, p. 288–289, not *T. cincta* Gmel., Syst. Nat., ed. 13, vol. 1, p. 2820 (1792).
1915 *Tipula iroquois* Alex. Insec. Inscit. Menst., vol. 3, p. 128.

The larva discussed below has never been reared and is mentioned here principally because of its interesting habitat. It is referred to *Tipula iroquois* with considerable doubt.

The larva lives among dense mats of an aquatic moss, a Hypnum (Rhynchostegium) of the *dilatatum* group, in the most rapid-flowing streams. At Coy Glen, Ithaca, New York, these larvae are especially frequent, often living at the brink of falls or rapids in the most rushing waters. A study of the structure of the larva reveals numerous small but prominent tubercles, which doubtless assist the insect in clinging to the moss stems. The gills are large, but no better developed than in many aquatic species of the genus that live in much less lotic conditions. The green color and the transverse rows of tubercles on the body give the larva a strong resemblance to its mossy habitat. The larvae are very sluggish and crawl but slowly, often appearing quite dead for long periods of time.

Associated with these larvae in Coy Glen, the following characteristic forms of insect life occur:

Plecoptera: a small species of Perlidae.
Ephemerida: Ephemeridae, such as Baetis, *Iron fragilis*, Ephemerella, and others.
Trichoptera: Ryacophilidae, Hydroptilidae, and other forms.
Neuroptera: Chauliodes larvae.
Diptera: Chironomidae, a few; Psychodidae, *Psychoda albitarsis* Banks; Stratiomyiidae; Anthomyiidae, *Limnophora torreyae* Joh.; and other groups.
Coleoptera: Parnidae, larvae of *Psephenus lecontei* (Lec.), and adult beetles of a species of Elmis in large numbers.

Up to the present time it has been found impossible to rear this larva to the adult condition, chiefly because of the constant need of well-aërated water and the difficulty of supplying it. By placing the larvae in the folds of moistened cheesecloth, it was possible on one occasion to carry the species to the pupal state, but no further. It will be of interest to ascertain the identity of this conspicuous larva.

Larva.— Length, 24–25 mm.
Diameter, 2.6–3 mm.

Coloration above, dark green with a brown pattern; beneath, light green with indistinct transverse brown lines; on dorsum a pale longitudinal mark on sides of posterior ring, crossing sutures between segments onto extreme base of anterior ring of following segment, the dark area of each segment thus appearing cruciform, this cross-shaped mark spotted and marbled with darker in transverse rows; base of gills and center of spiracular disk light green in living, healthy larvae.

Form moderately terete, each segment with transverse rows of small, prominent tubercles, some of which are provided with setae. On dorsum of posterior ring a subterminal row of six tubercles, the middle one on each side with two setae, the remaining four tubercles unisetose; two rows of smaller naked tubercles at base and middle of posterior annulus; basal annulus with four transverse rows of small naked tubercles; pleurites with three tubercles, a small seta on basal ring ventrad of basal tubercle, and two setae on posterior ring ventrad and cephalad of posterior tubercle; sternites on posterior ring with six setae, four on anterior row, the two middle ones very tiny. Spiracular disk almost as in *T. collaris*, *T. ignobilis*, and similar species, surrounded by six lobes fringed with moderately long hairs; inner face of lobes somewhat pale; ventral lobes with a narrow, capillary, dark brown line, extending from tip toward base; lobes narrowly and more or less indistinctly margined with brown; two brown spots at base of each ventral lobe, underneath each spiracle; dorsal and lateral lobes jutting backward at tips into fleshy conical points. Spiracles circular, moderately large, separated by a distance about equal to one and one-half diameter of one. Anal gills with eight branches, rather short and stout, with two lateral divergent branches on either side and an inner pair with one ventral and one posterior branch (Plate XCII, 512).

Head capsule and mouth parts of almost normal tipuline appearance. Mentum with outer plate forming the unusually long apical point, inner plate adding three teeth on either side, margins bulging. Antenna with apical papillae somewhat flattened, surrounded by three sense pegs.

(Described from abundant specimens, Coy Glen, Ithaca, New York, April 23, 1914.)

Tipuline No. 2

The larva discussed below is known only from a single, apparently fully grown, specimen. The writer has no clue as to which species it represents, altho from the larval structure it is obviously allied to *Tipula selene* Meig. of Europe.

Larva.— Length, 23 mm.
Diameter, 3 mm.

Coloration, a rather uniform pale yellowish or reddish brown.

Body covered with a rather sparse, long pubescence, setae unusually long and powerful. Chaetotaxy as follows: tergites (Plate XCVI, 534) with two strong lateral setae near posterior margin and an additional one at extreme lateral margin of ring; pleural setae, one on basal ring, two, one behind the other, on posterior ring; sternites with a transverse pair of powerful setae near extreme lateral margin, and two anterior pairs of much smaller setae. Spiracular disk (Plate XCVI, 535) with four elongated, cylindrical, chitinized horns which are narrowed to the acute, blackened, slightly curved tips; longer dorsal pair rather closely approximated, lying almost parallel, with tips a little curved dorsad; shorter and more slender lateral horns directed ventrad at tips, at base on inner face with a powerful seta, the large black spiracles lying above base of lateral horns; ventral lobes, if present, very blunt and indistinct. Anal gills not protruded in the only specimen available.

Head capsule and mouth parts rather normal but showing the following points of difference from the usual Tipula type: Mentum almost completely split, apical point long and narrow; the three lateral teeth on either side blunt, lateral pair tending to be reduced.

Hypopharynx with five blunt teeth. Antenna short, stout, length only about twice diameter, at tip with a subglobular, feebly chitinized papilla.

(Described from a single larva found beneath a stone in a field near Taughannock Falls, Tompkins County, New York, May 1, 1912.)

Genus **Nephrotoma** Meigen (Gr. *kidney + I cut*)

1800 *Pales* Meig. Nouv. Class. Mouch., p. 14 (*nomen nudum*).
1803 *Nephrotoma* Meig. Illiger's Mag., p. 262.
1834 *Pachyrrhina* Macq. Hist. Nat. Ins., Dipt., vol. 1, p. 88.

The large genus Nephrotoma, including some one hundred and fifty described species, is very close to Tipula in all respects. The writer cannot attempt to separate the immature stages of the genus from those of Tipula, on the scanty material that has been available for study.

In Europe, Beling and others have described the life histories of about eight of the commoner species. The following species live in earth, beneath a covering of leaf mold: *analis* (Schum.), *cornicina* (Linn.), *lineata* (Scop.), *maculata* (Meig.), *lunulicornis* (Schum.), *pratensis* (Linn.). The following have been described as living in decaying wood, some of the records apparently being in error: *cornicina* (Linn.), *crocata* (Linn.), *lineata* (Scop.), *quadrifaria* (Meig.). Some of the species are injurious to young seedlings, especially those of coniferous plants.

In North America the commonest species, *N. ferruginea* (Fabr.), has been discussed several times in its economic relations to agriculture. Hart (1898 [1895]: 218–219) gives an excellent description of the immature stages, while Malloch (1915–17 b: 206) gives supplementary notes and figures of the same species. The immature stages live in sand or earth. *N. virescens* (Loew) was bred from a larva found in moss on Plummers Island, Maryland, on April 5, 1913, by R. C. Shannon. *N. eucera* (Loew) and *N. polymera* (Loew) have been reared from larvae taken under leaf mold in woods by Mabel M. Alexander.

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EXPLANATION OF ABBREVIATIONS USED ON PLATES

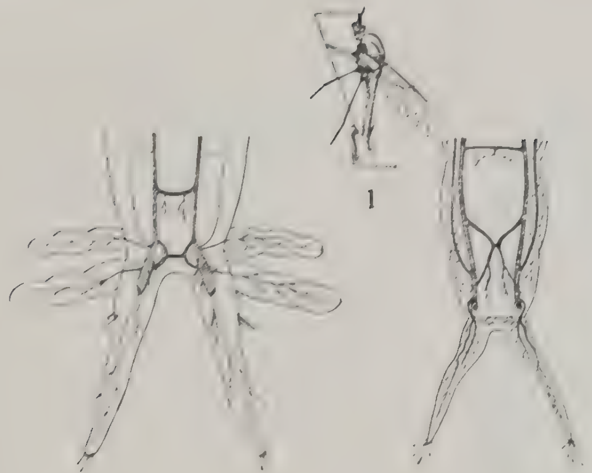
A=antenna
C=cardo
Lb=labium, or labial lobes
M=mentum
Md=mandible
Mx=maxilla
P=palpus, or palpal sheath
Pl=pleuron
PM=prementum
S=stipes
SM=submentum
Sp=spiracle
St=sternite
T=tergite

Memoir 34, *An Economic Study of Farm Layout*, the fourth preceding number in this series of publications, was mailed on January 31, 1921.

Memoir 35, *Some Effects of Potassium Salts on Soils*, the third preceding number in this series of publications, was mailed on January 29, 1921.

Memoir 36, *Resistance of the Roots of Some Fruit Species to Low Temperature*, the second preceding number in this series of publications, was mailed on January 19, 1921.

Memoir 37, *A Modified Babcock Method for Determining Fat in Butter*, the next preceding number in this series of publications, was mailed on December 10, 1920.



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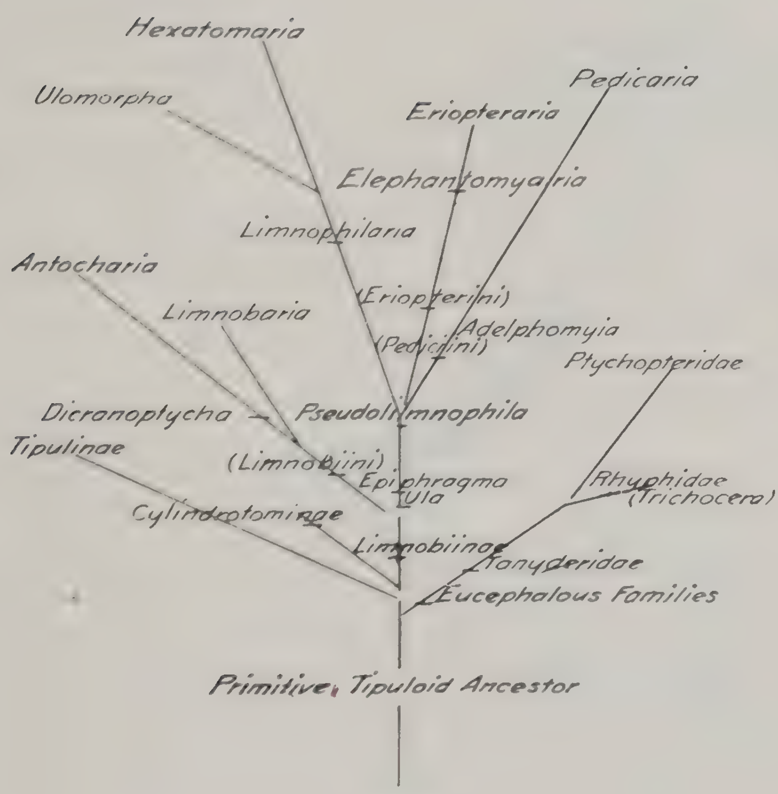
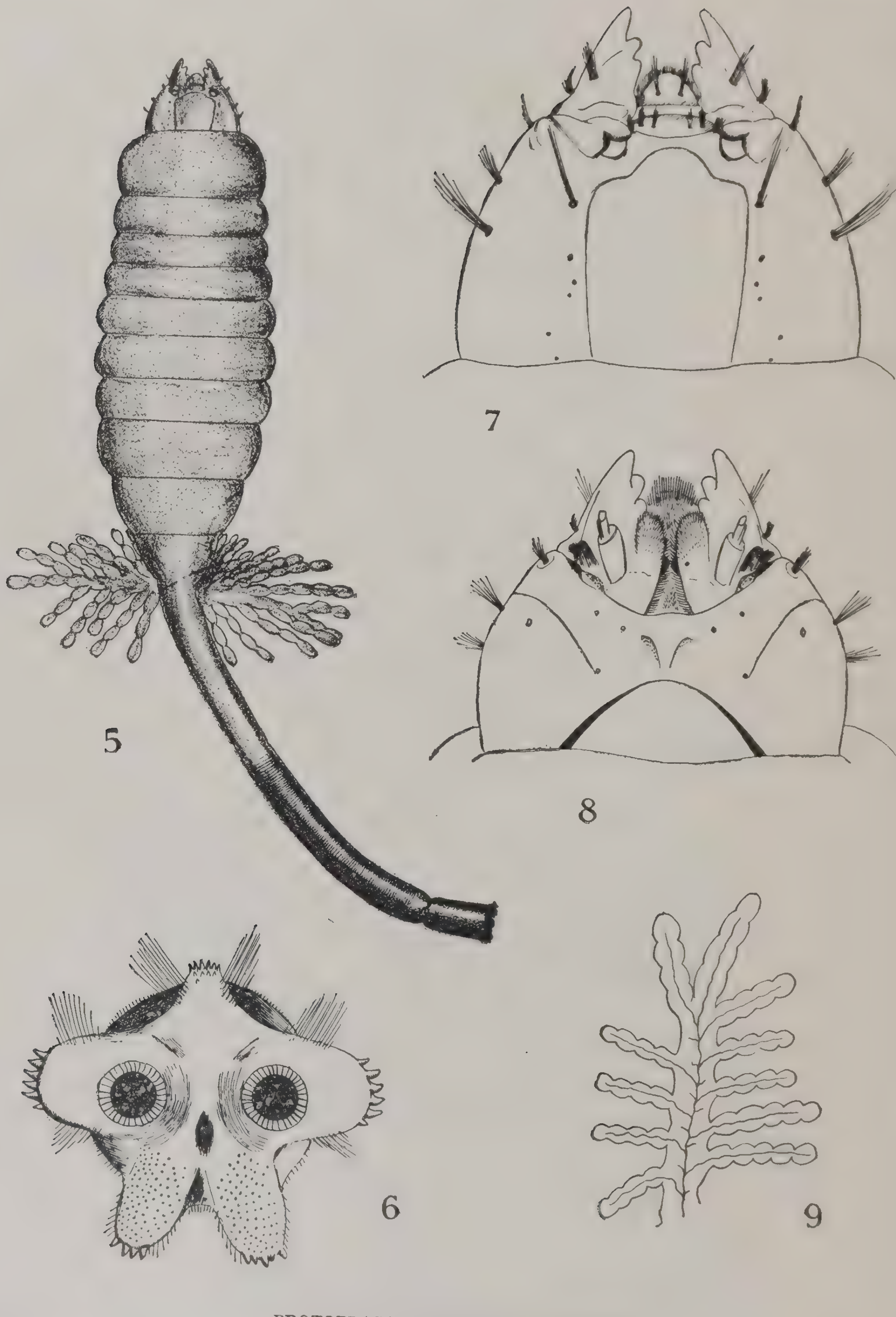


4

1, *Eriocera spinosa* emerging from pupal hull.

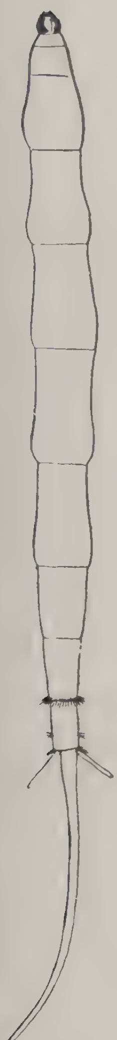
2–3, Spiracular disk and tracheation of larvae: 2, *Antocha saxicola* (apneustic); 3, *Dicranota bimaculata* (metapneustic), after Miall

4, Phylogenetic tree



PROTOPLASA FITCHII, SUPPOSITION

5, Dorsal aspect; 6, spiracular disk; 7, head, dorsal aspect; 8, head, ventral aspect; 9, anal gill



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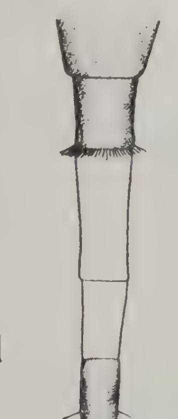

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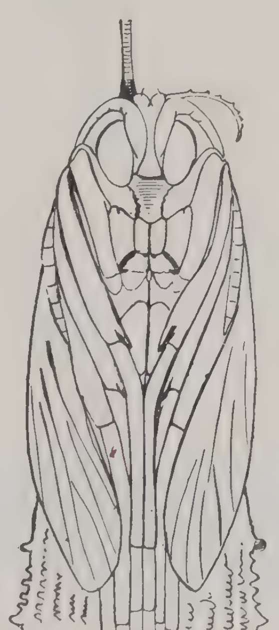

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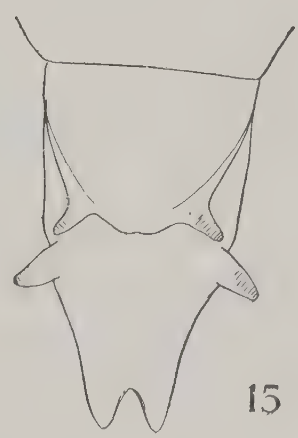

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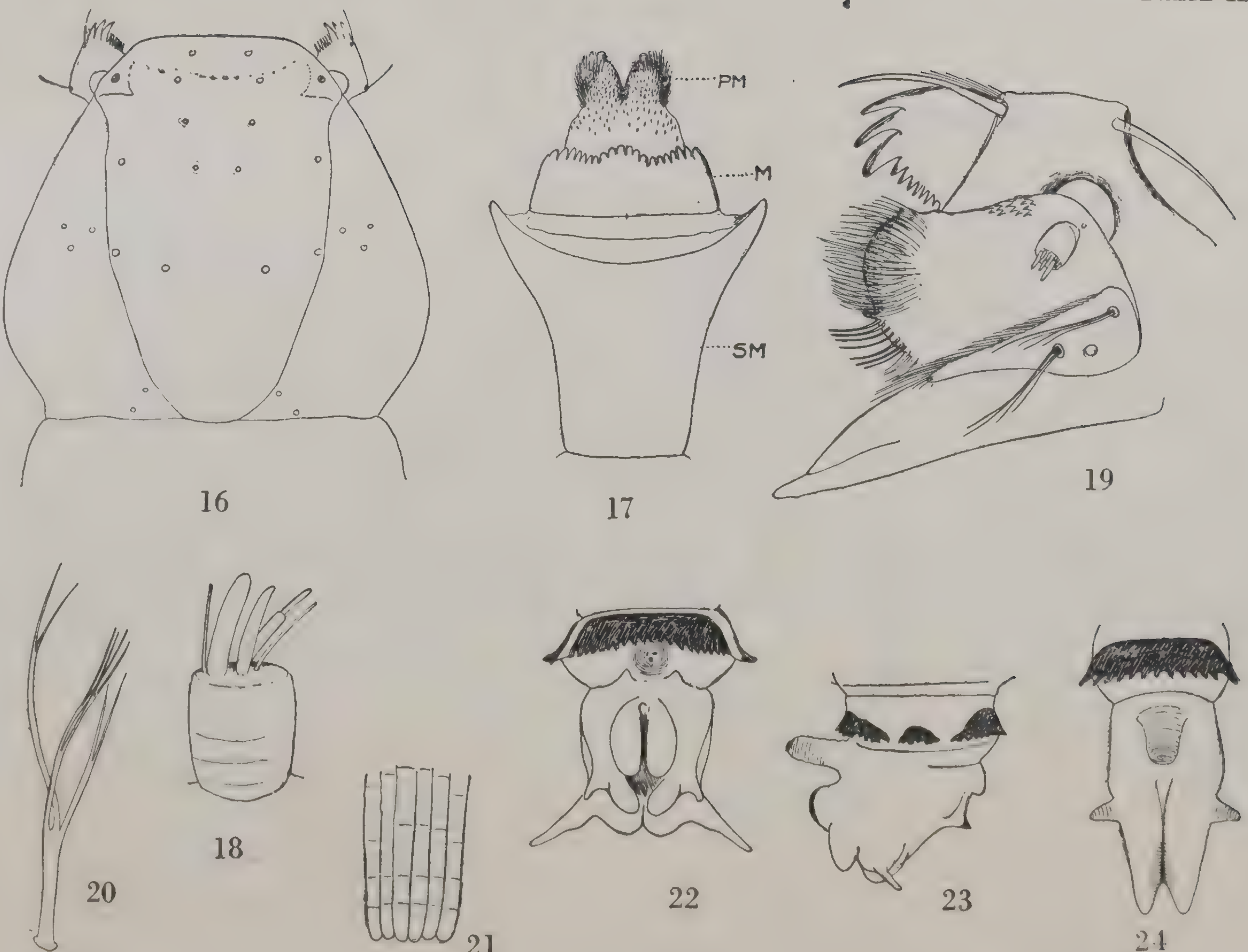
PTYCHOPTERA RUFOCINCTA

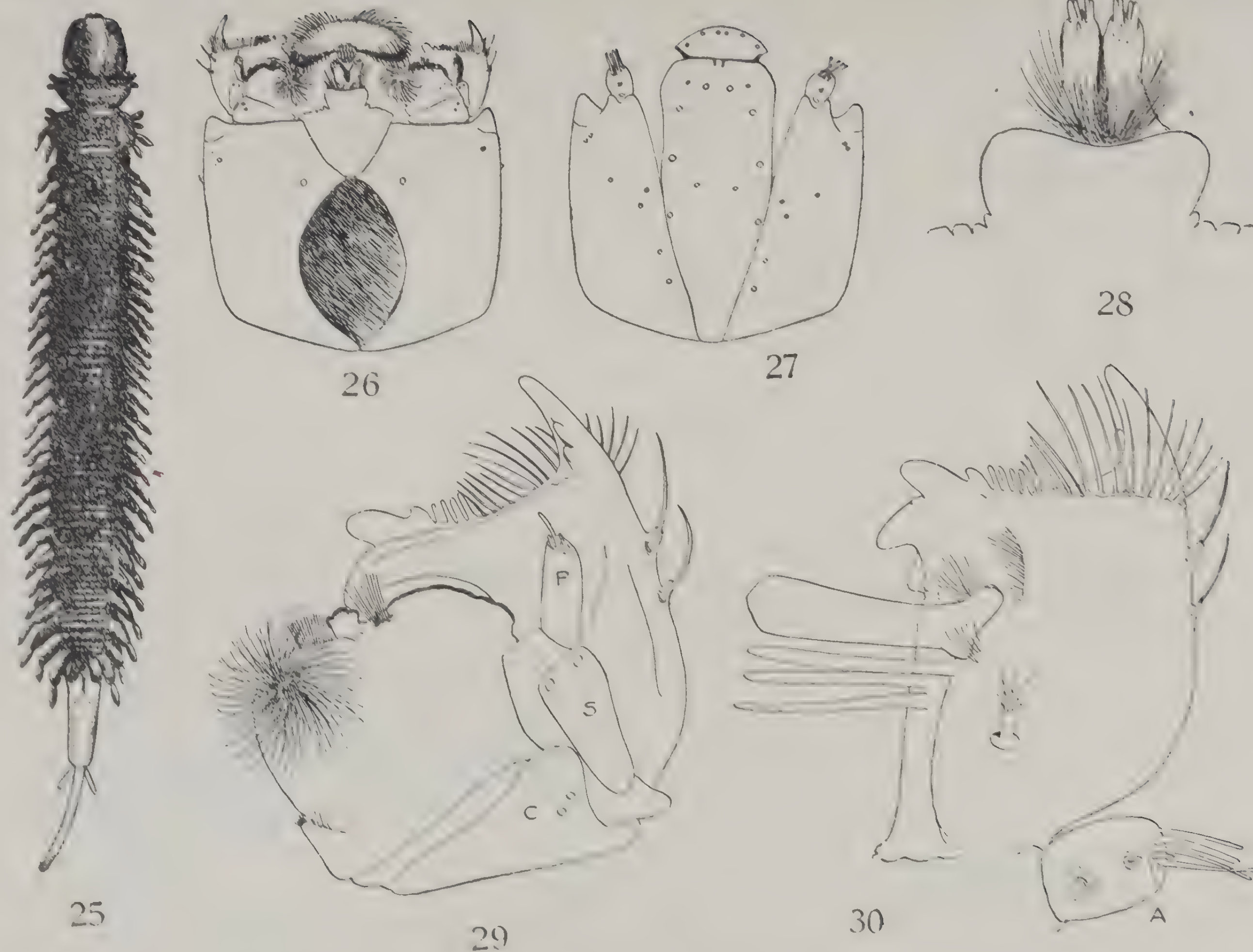
Larva: 10, dorsal aspect; 11, breathing tube extended; 12, head, ventral aspect
Pupa: 13, lateral aspect; 14, ventral aspect; 15, female cauda, ventral aspect



PTYCHOPTERA RUFOCINCTA

Larva: 16, head, dorsal aspect; 17, labium, ventral aspect; 18, antenna; 19, mandible and maxilla; 20, plumose hairs of head

Pupa: 21, arrangement of leg sheaths; 22, male cauda, dorsal aspect; 23, male cauda, lateral aspect; 24, female cauda, dorsal aspect



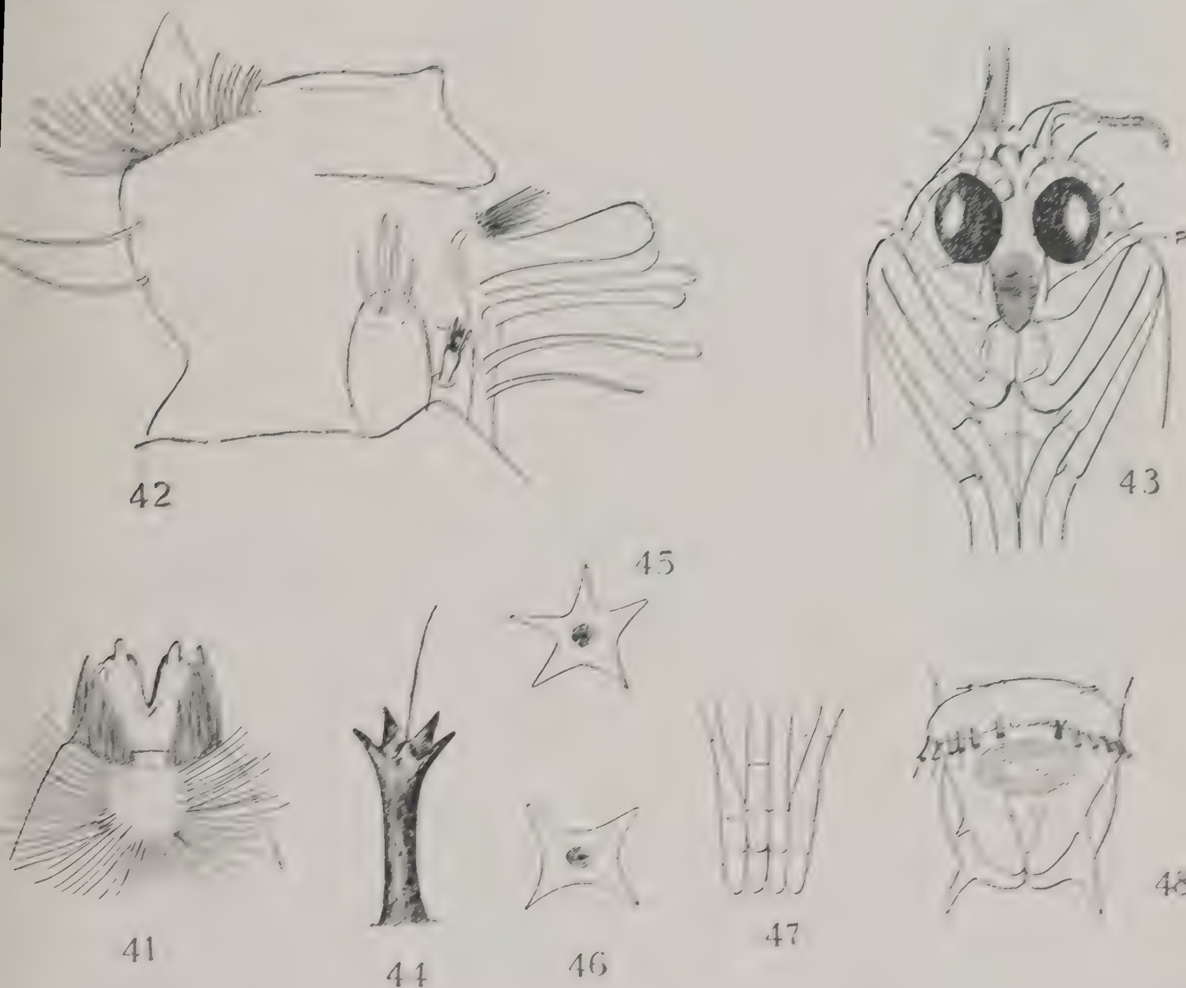
BITTACOMORPHELLA JONESI, LARVA

25, Dorsal aspect; 26, head, ventral aspect; 27, head, dorsal aspect; 28, labium, ventral aspect; 29, mandible and maxilla, ventral aspect; 30, mandible and antenna, dorsal aspect

BITTACOMORPHELLA JONESI

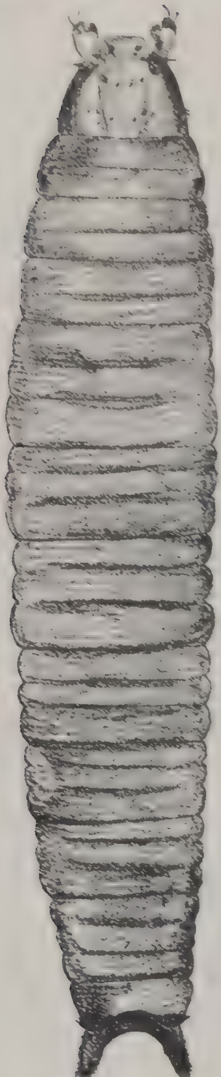
Larva: 31, labrum-epipharynx; 32, apex of pseudopod, and claw; 33, body projection; 34, body projection, enlarged; 35, branched hairs on body

Pupa: 36, mouth parts; 37, arrangement of leg sheaths; 38, types of abdominal tubercles; 39, male cauda, dorsal aspect; 40, male cauda, ventral aspect



BITTACOMORPHA CLAVIPES

Larva: 41, labium; 42, mandible and antenna, dorsal aspect
Pupa: 43, ventral aspect; 44-46, types of abdominal tubercles; 47, arrangement of leg sheaths; 48, male cauda, dorsal aspect



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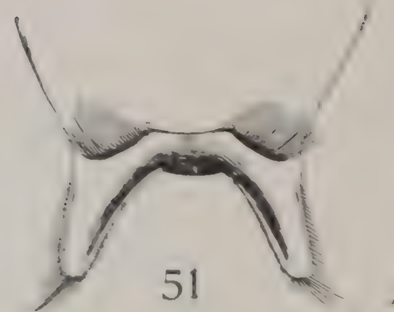

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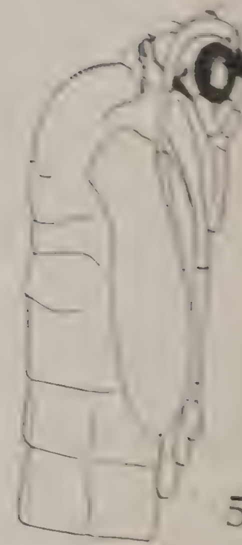

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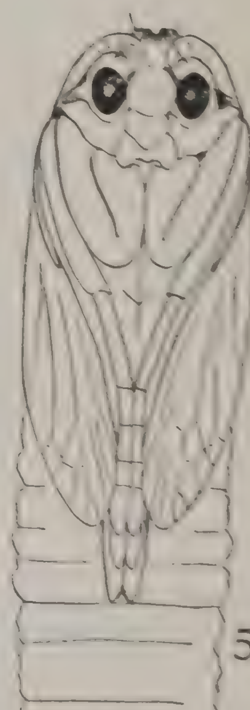

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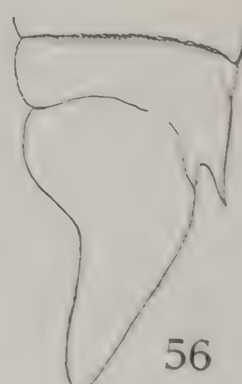

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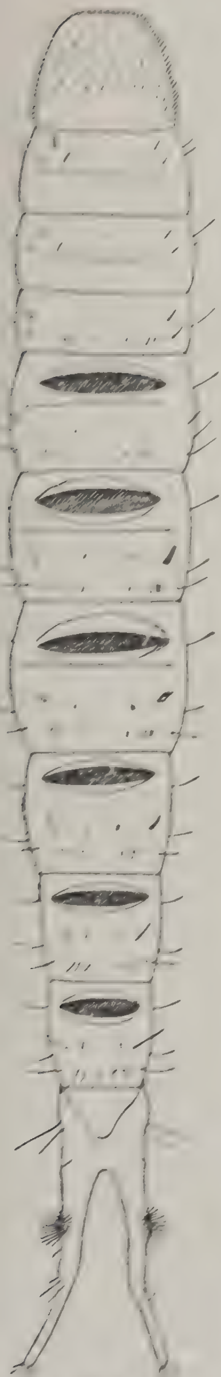
TRICHOCERA SP? (REGELATIONIS, SUPPOSITION)

Larva: 49, dorsal aspect; 50, spiracular disk, lateral aspect; 51, spiracular disk, dorsal aspect; 52, head, ventral aspect (after De Meijere); 53, head, dorsal aspect (after De Meijere).
Pupa: 54, lateral aspect; 55, female, ventral aspect; 56, female cauda, lateral aspect



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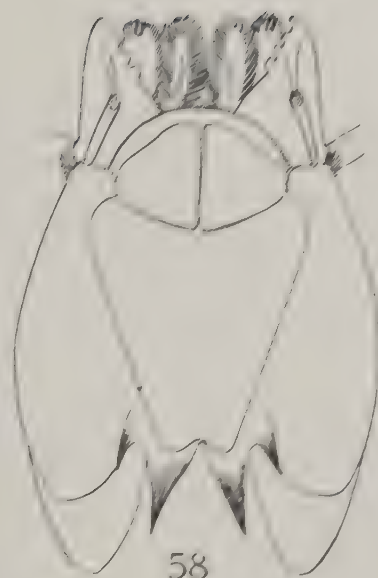

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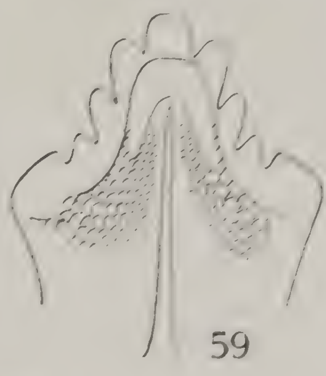

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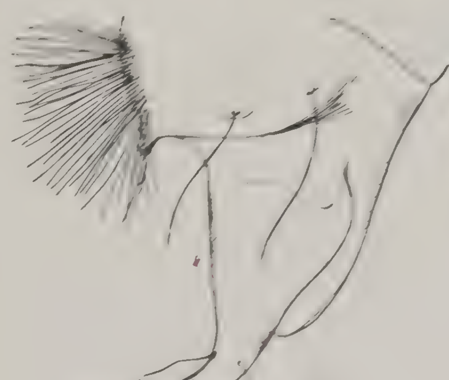

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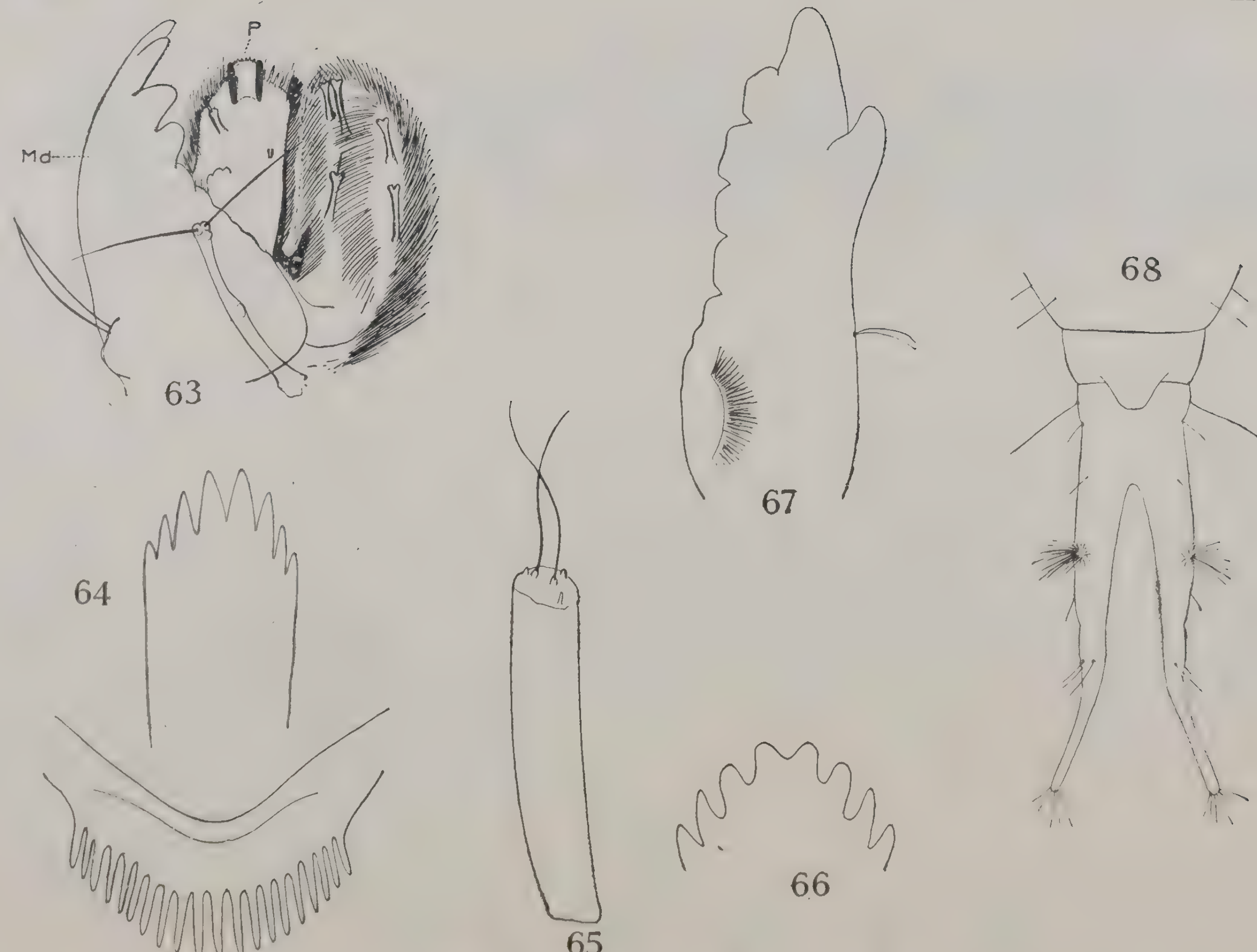
61

ANTOCHA SAXICOLA

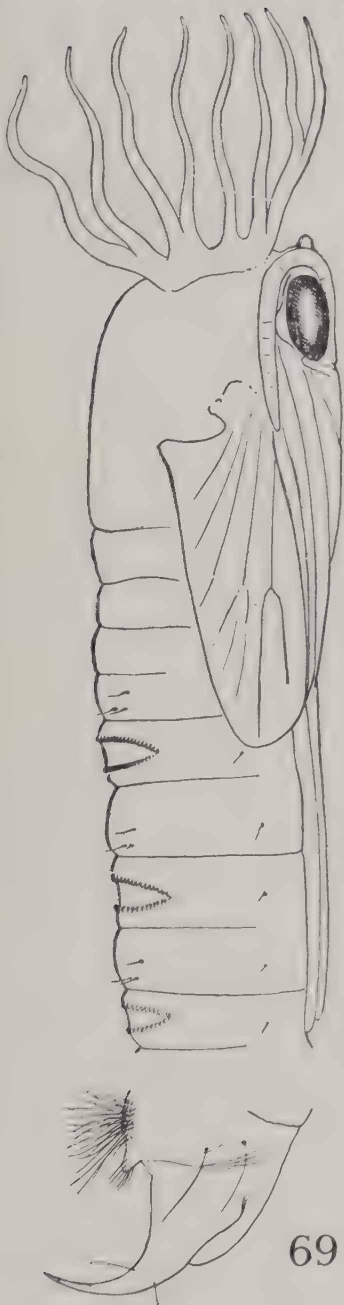
Larva: 57, dorsal aspect; 58, head capsule, dorsal aspect; 59, mentum

Pupa: 60, ventral aspect; 61, pronotal breathing horn, lateral aspect; 62, female cauda, lateral aspect



ANTOCHA SAXICOLA, LARVA

63, Mandible and maxilla, ventral aspect; 64, hypopharynx; 65, antenna; 66, mentum, aberration; 67, mandible; 68, spiracular disk, dorsal aspect



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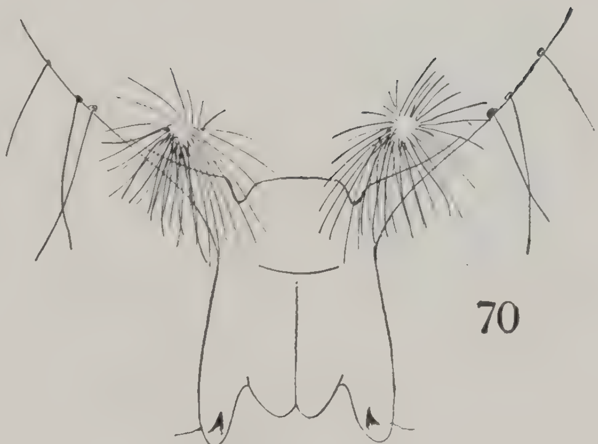

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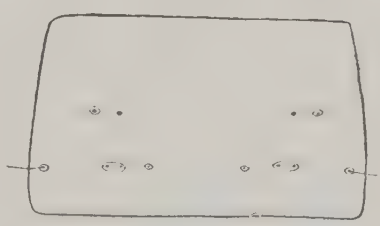

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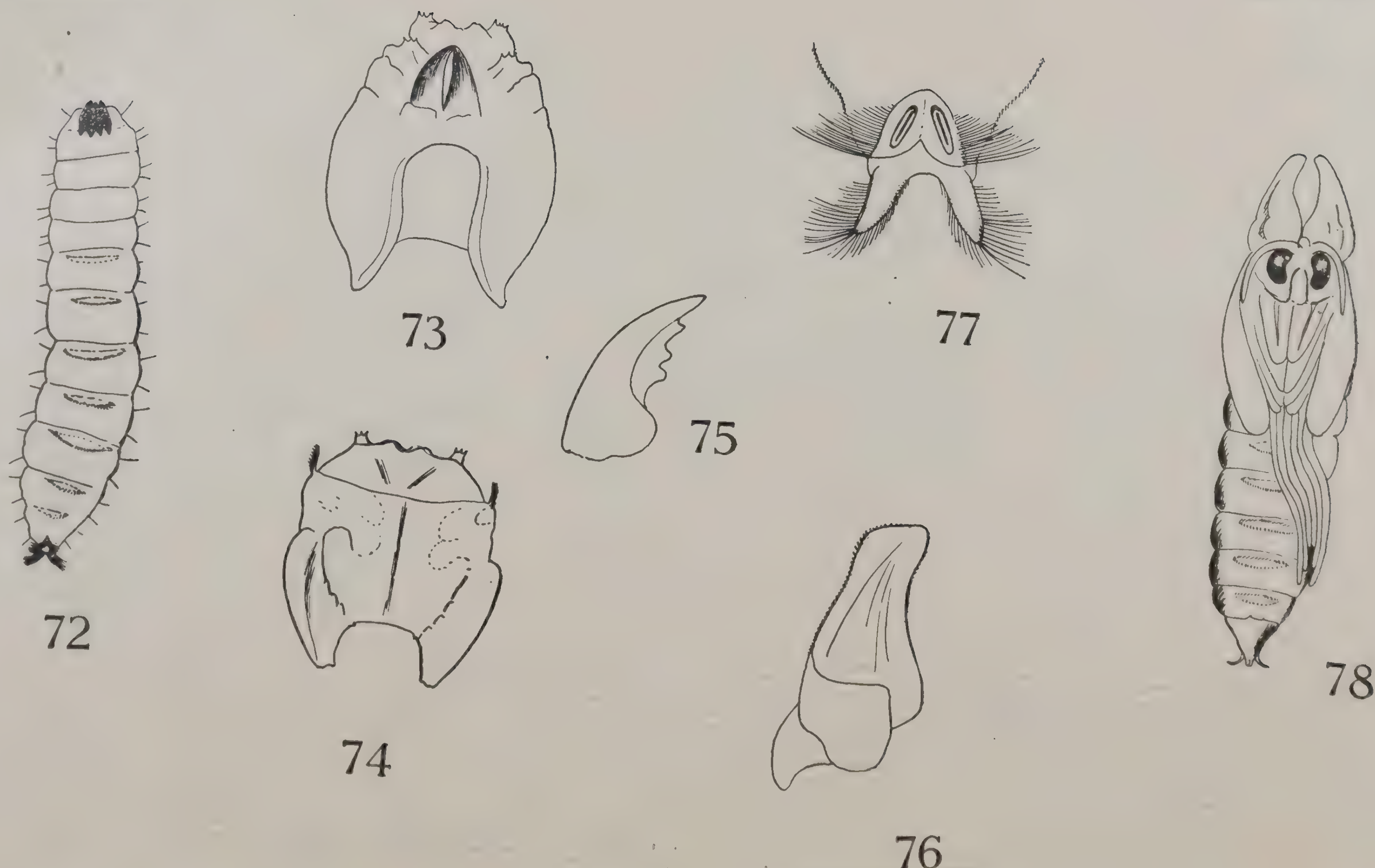
ANTOCHA SAXICOLA, PUPA

69, Lateral aspect; 70, male cauda, dorsal aspect; 71, fifth abdominal segment, dorsal aspect (diagrammatic)



ELLIPTERA OMISSA (AFTER MILK)

Larva: 72, dorsal aspect; 73, head capsule, ventral aspect; 74, head capsule, dorsal aspect; 75, mandible; 77, spiracular disk
Pupa: 76, pronotal breathing horn; 78, ventral aspect

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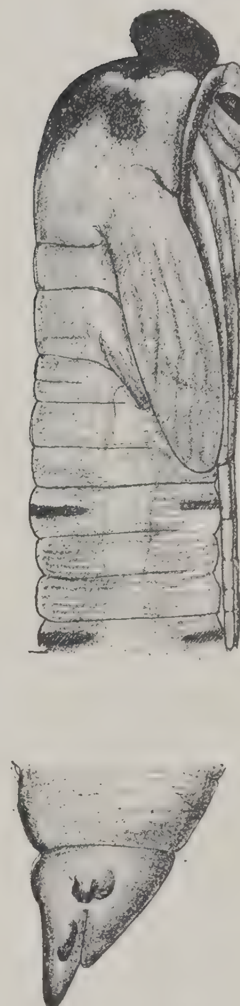
81



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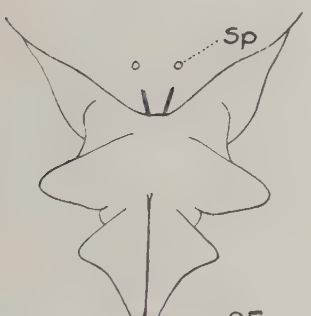

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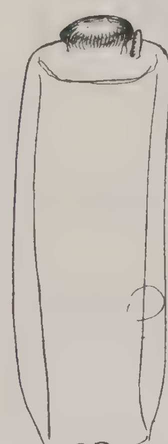

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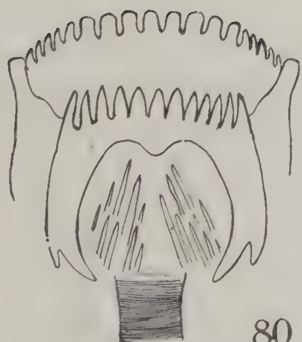

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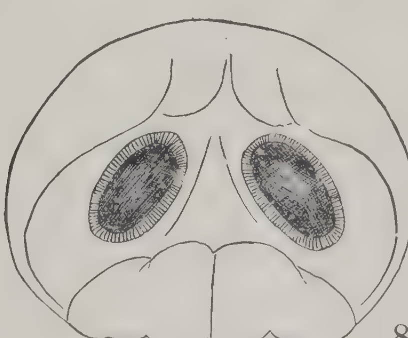

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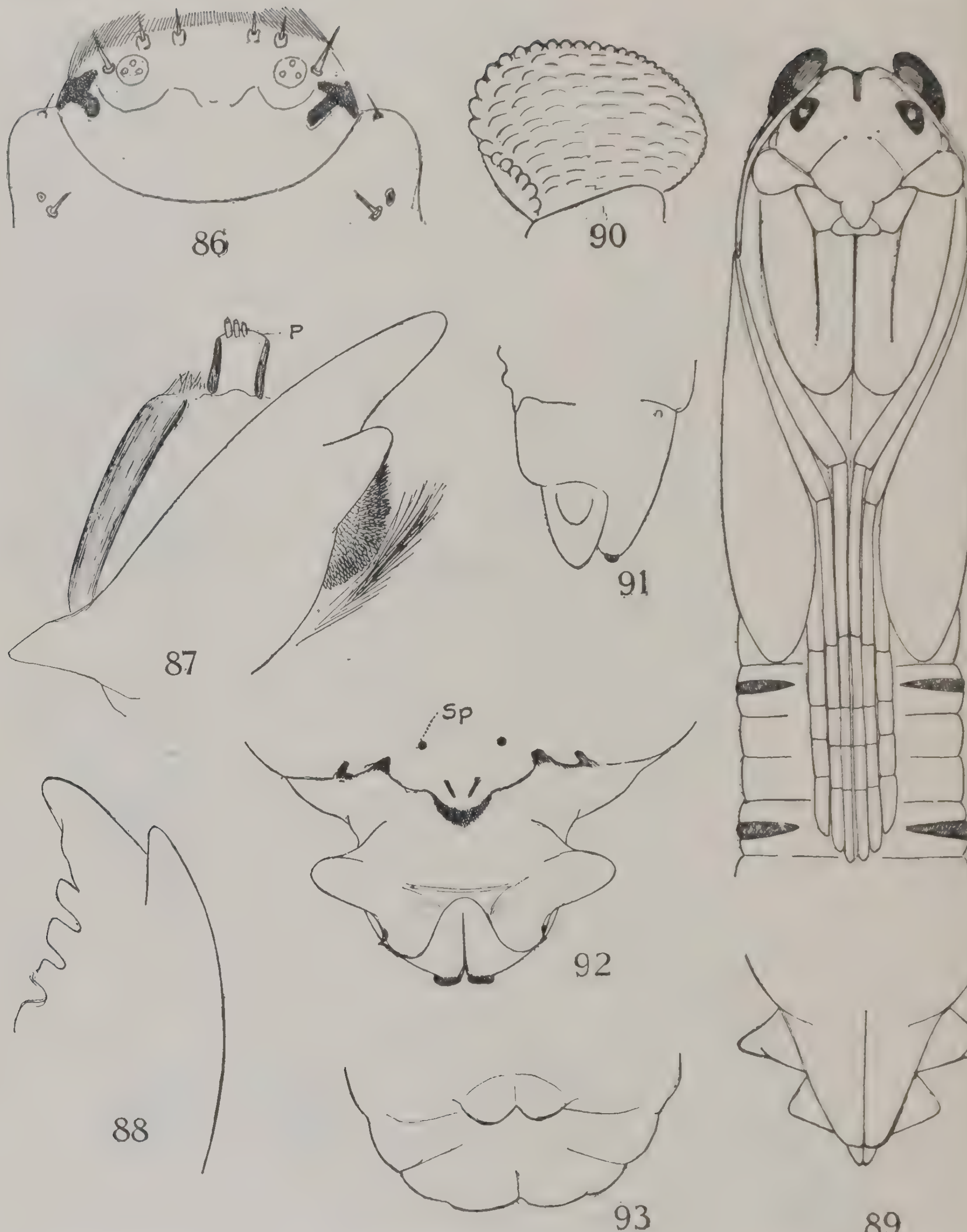
LIMNOBIA CINCTIPES

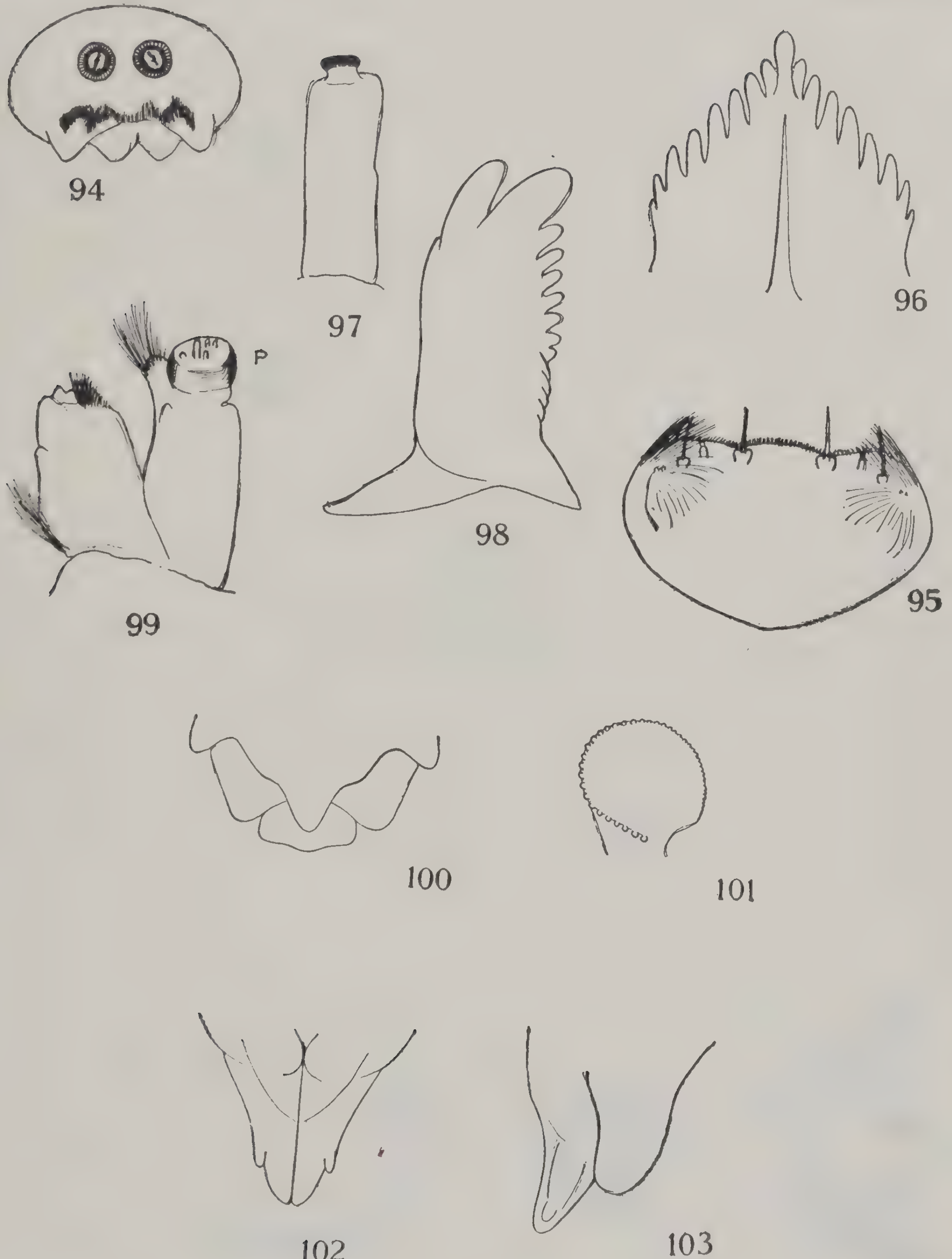
Larva: 79, head capsule, dorsal aspect; 80, hypopharynx; 81, mentum; 82, antenna; 83, spiracular disk
Pupa: 84, female, lateral aspect; 85, female cauda, dorsal aspect



LIMNOBIA CINCTIPES

Larva: 86, labrum-epipharynx; 87, mandible and maxilla; 88, mandible; 93, spiracular disk, dorsal aspect

Pupa: 89, female, ventral aspect; 90, pronotal breathing horn, lateral aspect; 91, male cauda, lateral aspect; 92, male cauda, dorsal aspect

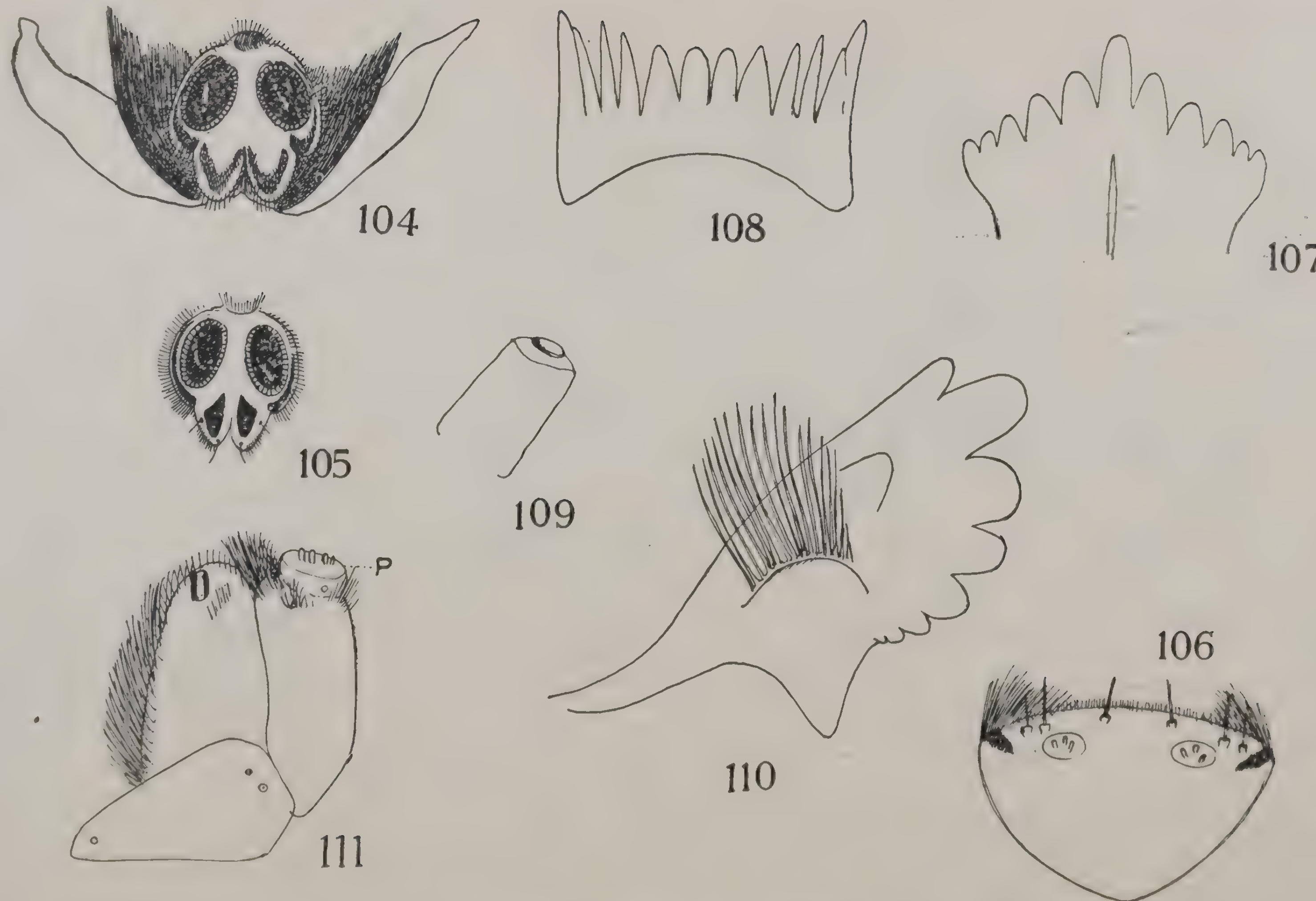


LIMNOBIA TRIOCELLATA AND L. FALLAX

Limnobia triocellata: 94, spiracular disk

Limnobia fallax, larva: 95, labrum-epipharynx; 96, mentum; 97, antenna; 98, mandible; 99, maxilla

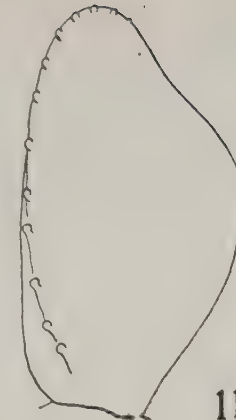
Limnobia fallax, pupa: 100, mouth parts; 101, pronotal breathing horn; 102, female cauda, dorsal aspect; 103, female cauda, lateral aspect



DICRANOMYIA BADIA AND D. STULTA

Dicranomyia badia: 104, spiracular disk
Dicranomyia stulta, larva: '05, spiracular disk; 106, labrum; 107, mentum; 108, hypopharynx; 109, antenna; 110, mandible; 111, maxilla

112



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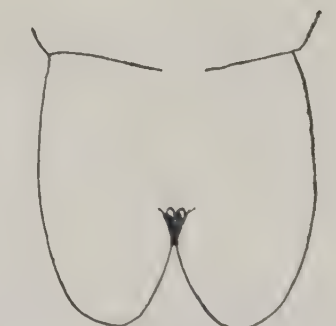

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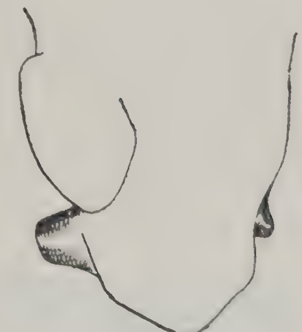
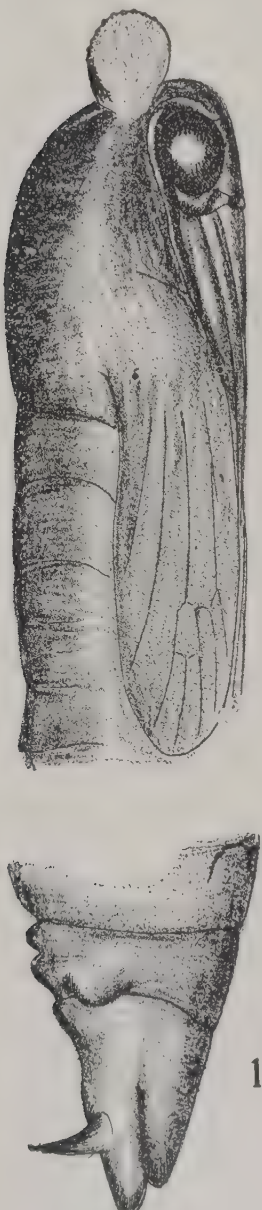


117

DICRANOMYIA STULTA, PUPA

112, Mouth parts; 113, pronotal breathing horn, dorsal aspect; 114, pronotal breathing horn, lateral aspect; 115, male cauda, dorsal aspect; 116, male cauda, ventral aspect; 117, male cauda, lateral aspect

119



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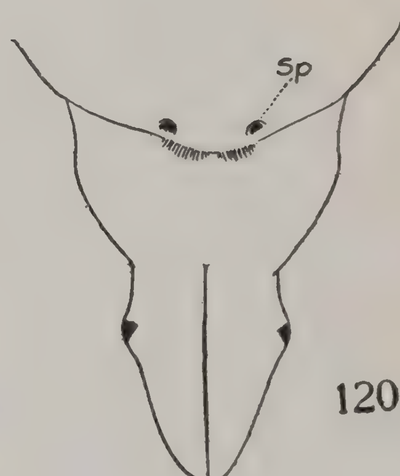
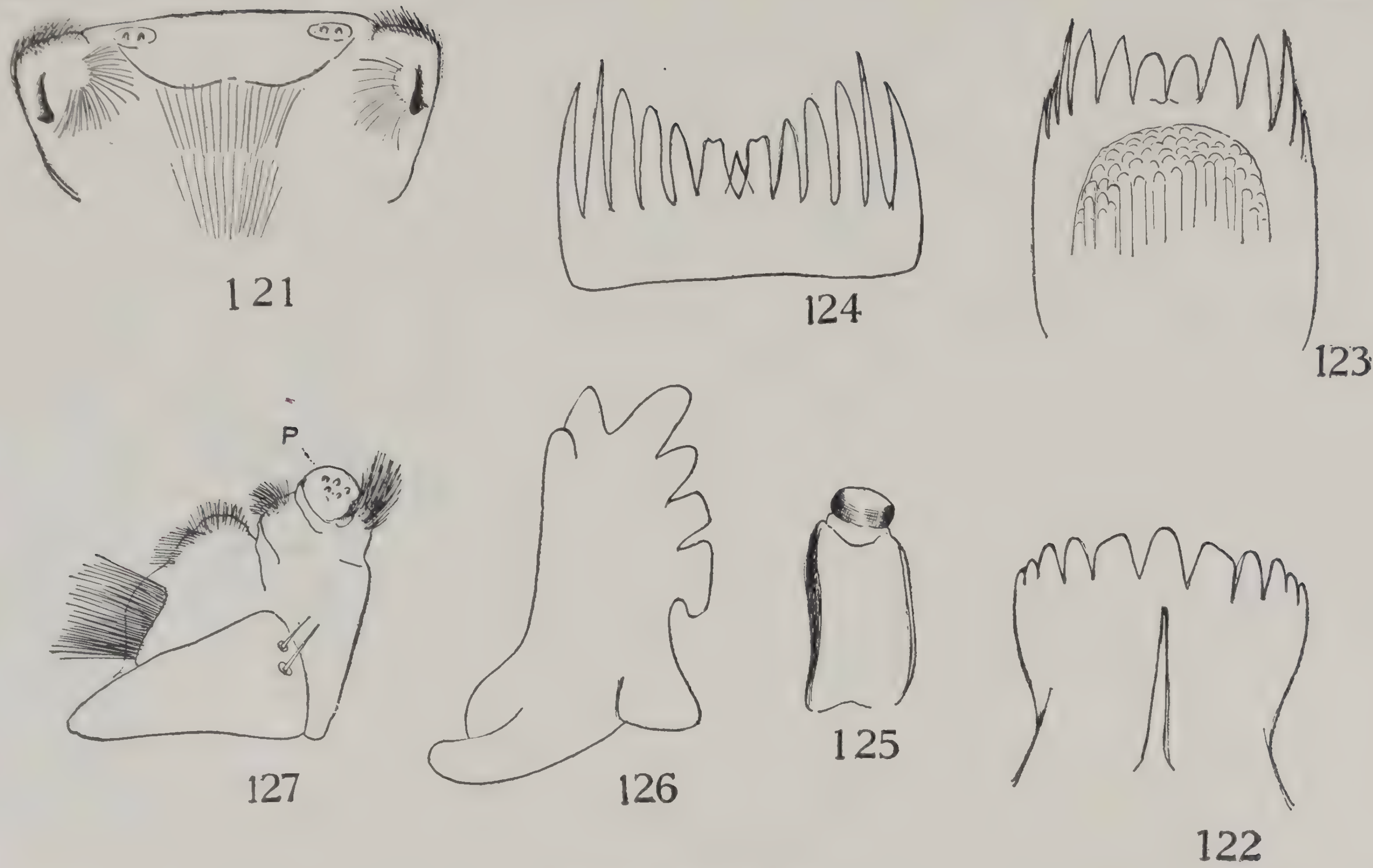


120

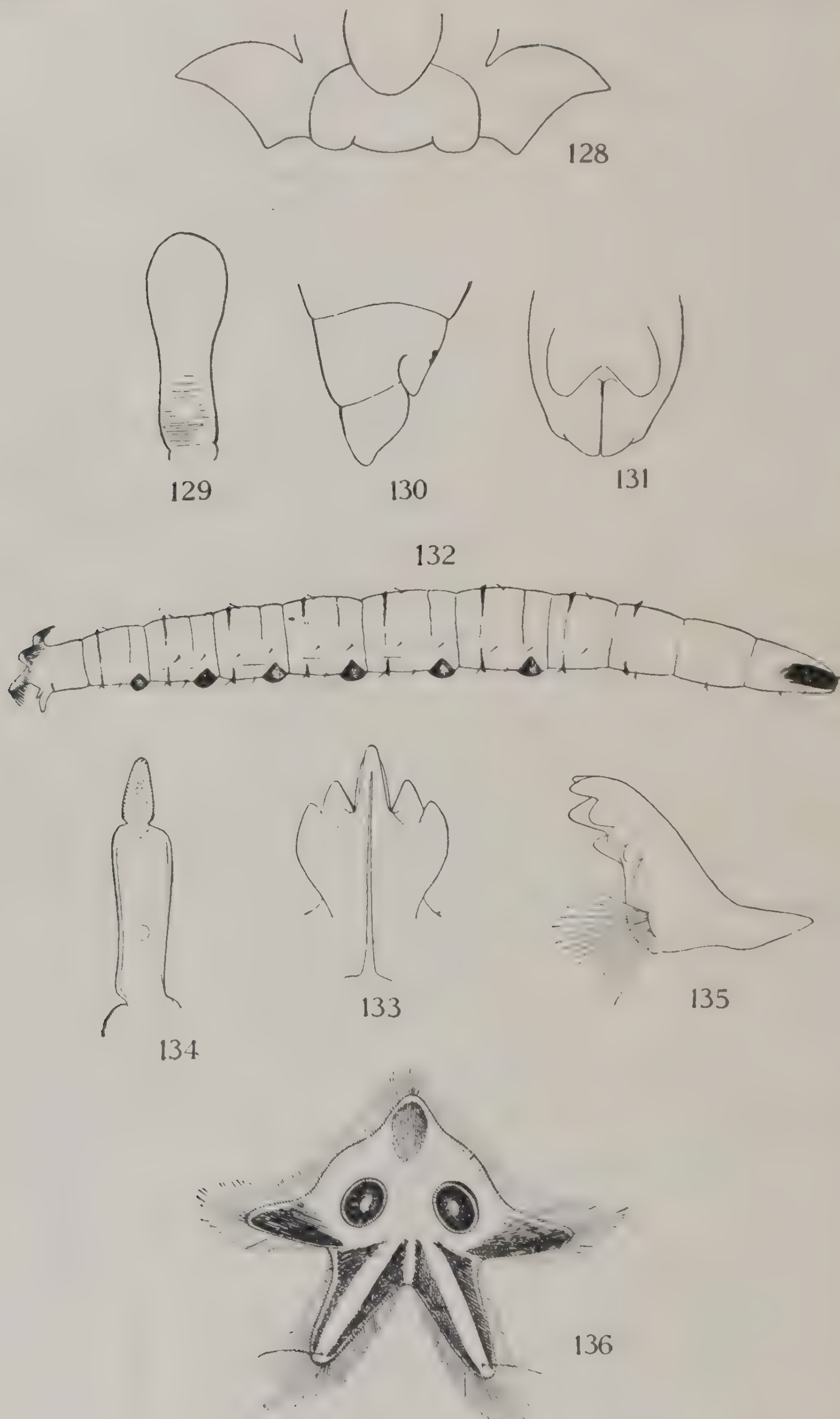
DICRANOMYIA BADIA, PUPA

118, Lateral aspect; 119, mouth parts; 120, female cauda, dorsal aspect



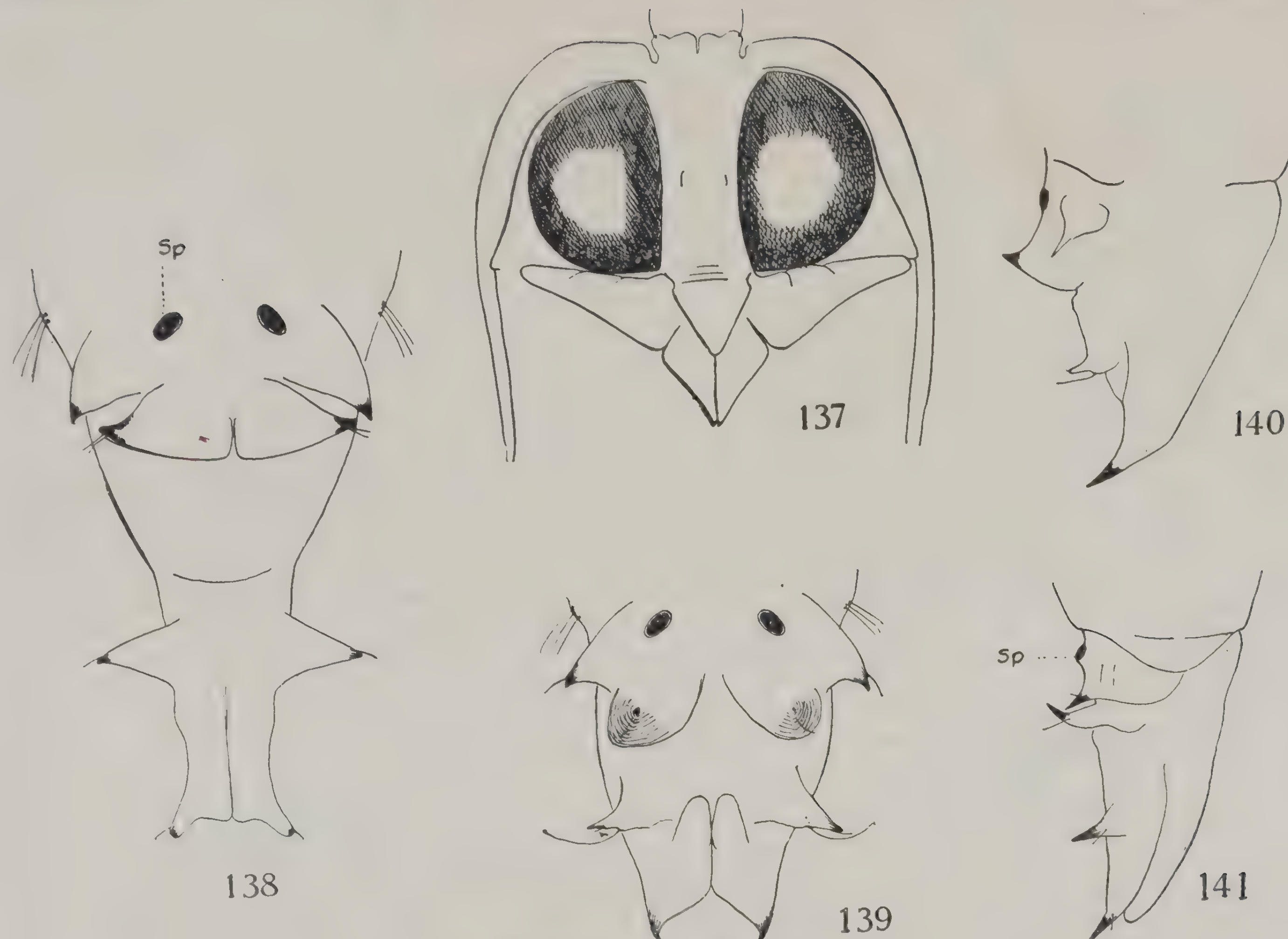
RHIPIDIA BRYANTI, LARVA

121, Labrum-epipharynx; 122, mentum; 123 and 124, hypopharynx; 125, antenna; 126, mandible; 127, maxilla



RHIPIDIA BRYANTI, RHAMPHIDIA MAINENSIS, AND RHAMPHIDIA FLAVIPES

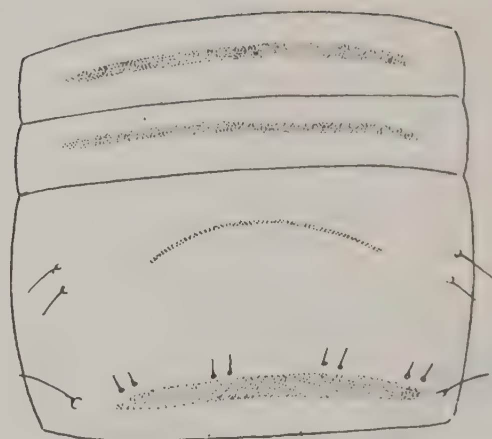
Rhipidia bryanti, pupa: 128, mouth parts; 129, pronotal breathing horn; 130, male cauda, lateral aspect; 131, male cauda, dorsal aspect
Rhamphidia mainensis, larva: 132, lateral aspect; 133, mentum; 135, mandible; 136, spiracular disk
Rhamphidia flavipes, larva: 134, antenna



RHAMPHIDIA FLAVIPES, PUPA

137, Head of male, ventral aspect; 138, female cauda, dorsal aspect; 139, male cauda, dorsal aspect; 140, male cauda, lateral aspect; 141, female cauda, lateral aspect

142



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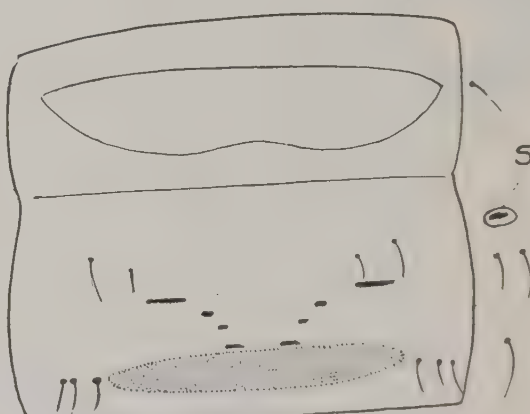
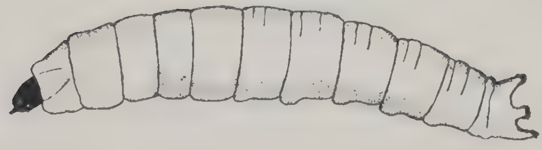


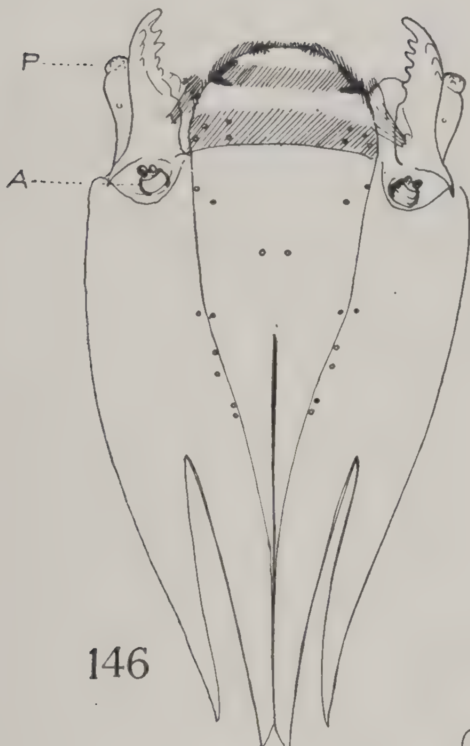
144

RHAMPHIDIA FLAVIPES, PUPA

142, Lateral aspect; 143, fifth abdominal segment, dorsal aspect (diagrammatic); 144, fifth abdominal segment, ventral aspect (diagrammatic)

145





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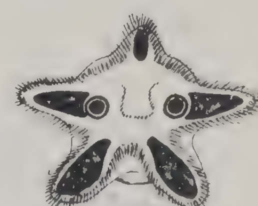
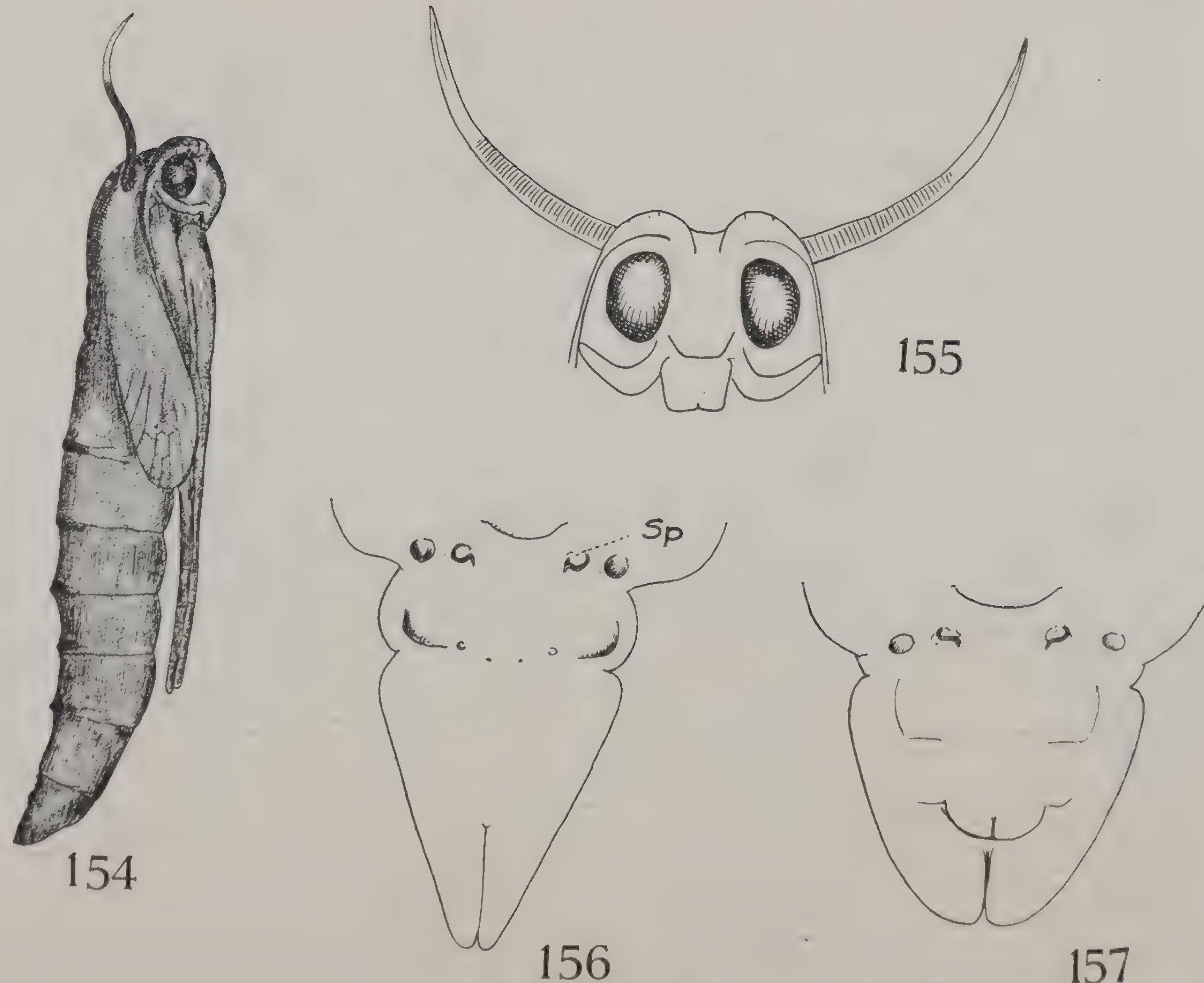


153

ULA ELEGANS, LARVA

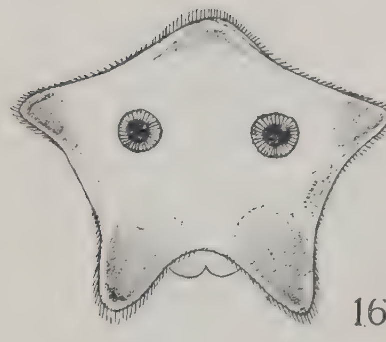
145, Lateral aspect; 146, head capsule, dorsal aspect; 147, labrum-epipharynx; 148, mentum 149, antenna; 150, mandible, lateral aspect; 151, mandible. from inside; 152, maxilla; 153, spiracular disk



ULA ELEGANS, PUPA

154, Female, lateral aspect; 155, head, ventral aspect; 156, female cauda, dorsal aspect; 157, male cauda, dorsal aspect

158



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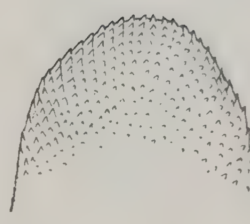

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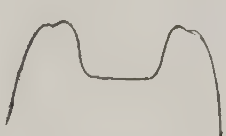

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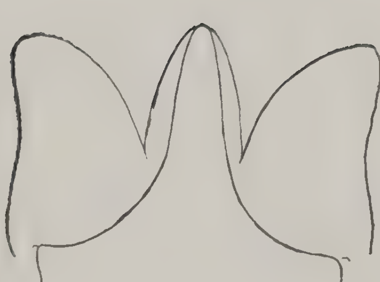

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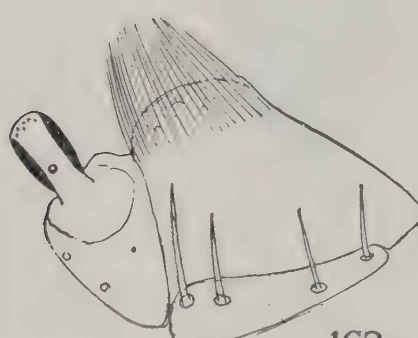


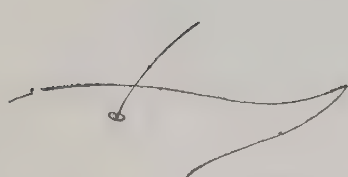
162

EPIPHRAGMA SOLATRIX, LARVA

158, Head capsule, ventral aspect; 159, mentum; 160, prementum; 161, hypopharynx; 162, maxilla; 163, spiracular disk

164

166



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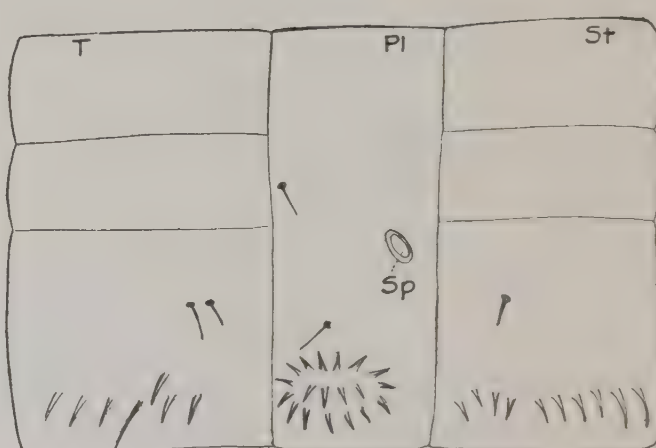

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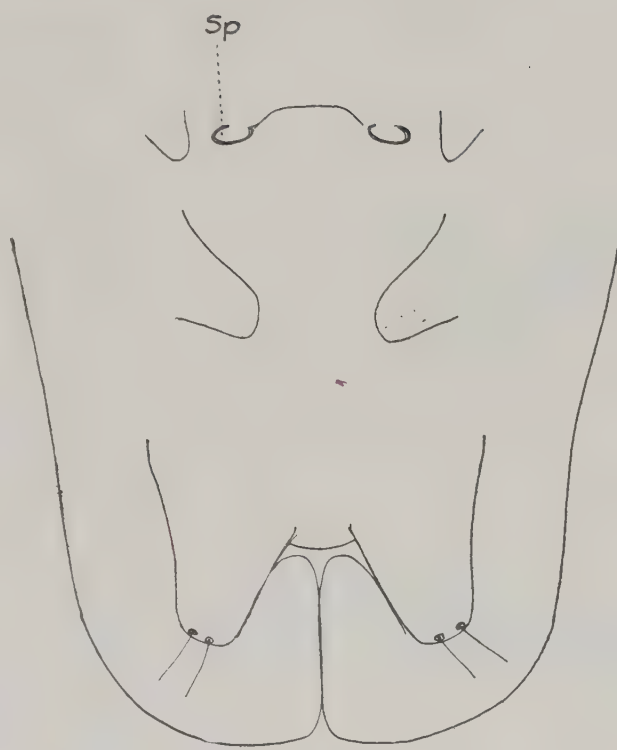
EPIPHRAGMA SOLATRIX AND E. FASCIPENNIS

Epiphragma solatrix, pupa: 164, lateral aspect; 166, head of male, ventral aspect; 167, fifth abdominal segment (diagrammatic)

Epiphragma fascipennis, pupa: 165, cephalic crest, lateral aspect



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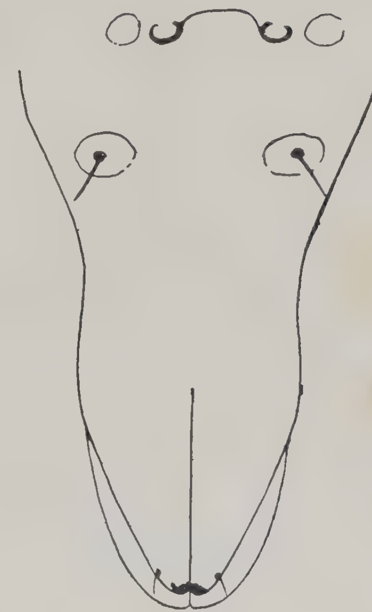

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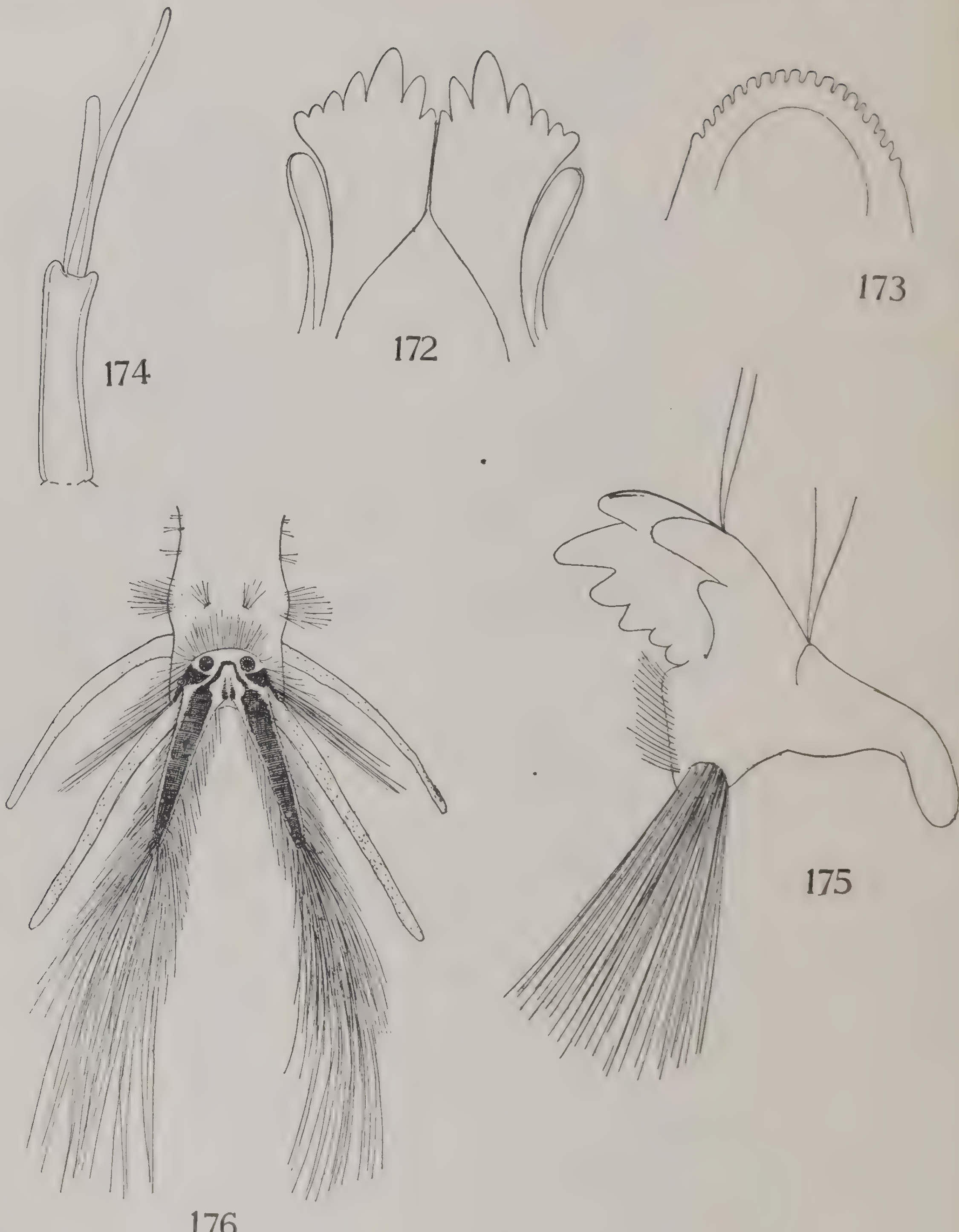
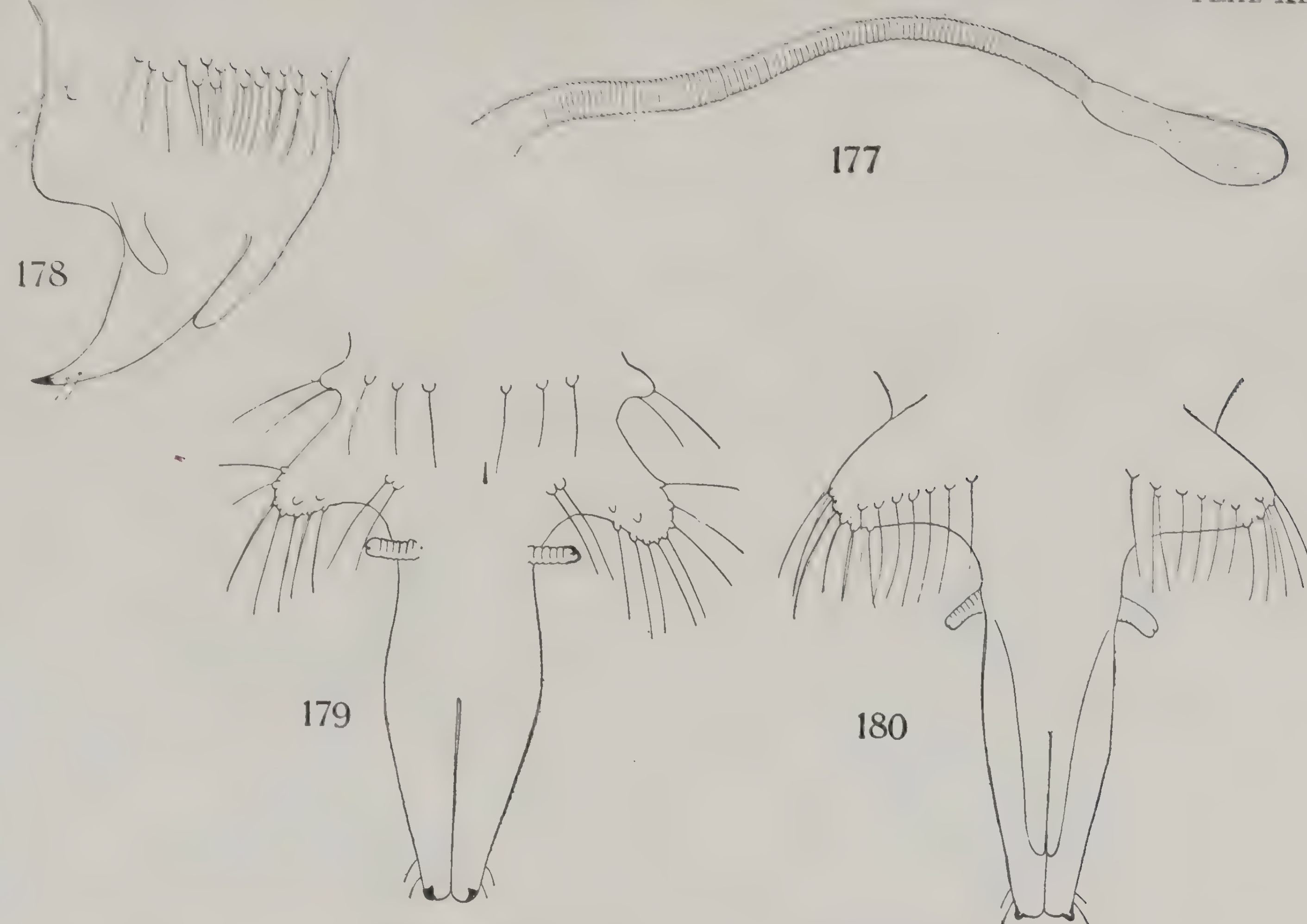
EPIPHRAGMA FASCIPENNIS AND E. SOLATRIX

Epiphragma fascipennis: 168, larva, labrum; 169, pupa, male cauda, dorsal aspect
Epiphragma solatrix, pupa: 170, male cauda, dorsal aspect; 171, female cauda, dorsal aspect



PSEUDOLIMNOPHILA LUTEIPENNIS AND P. INORNATA

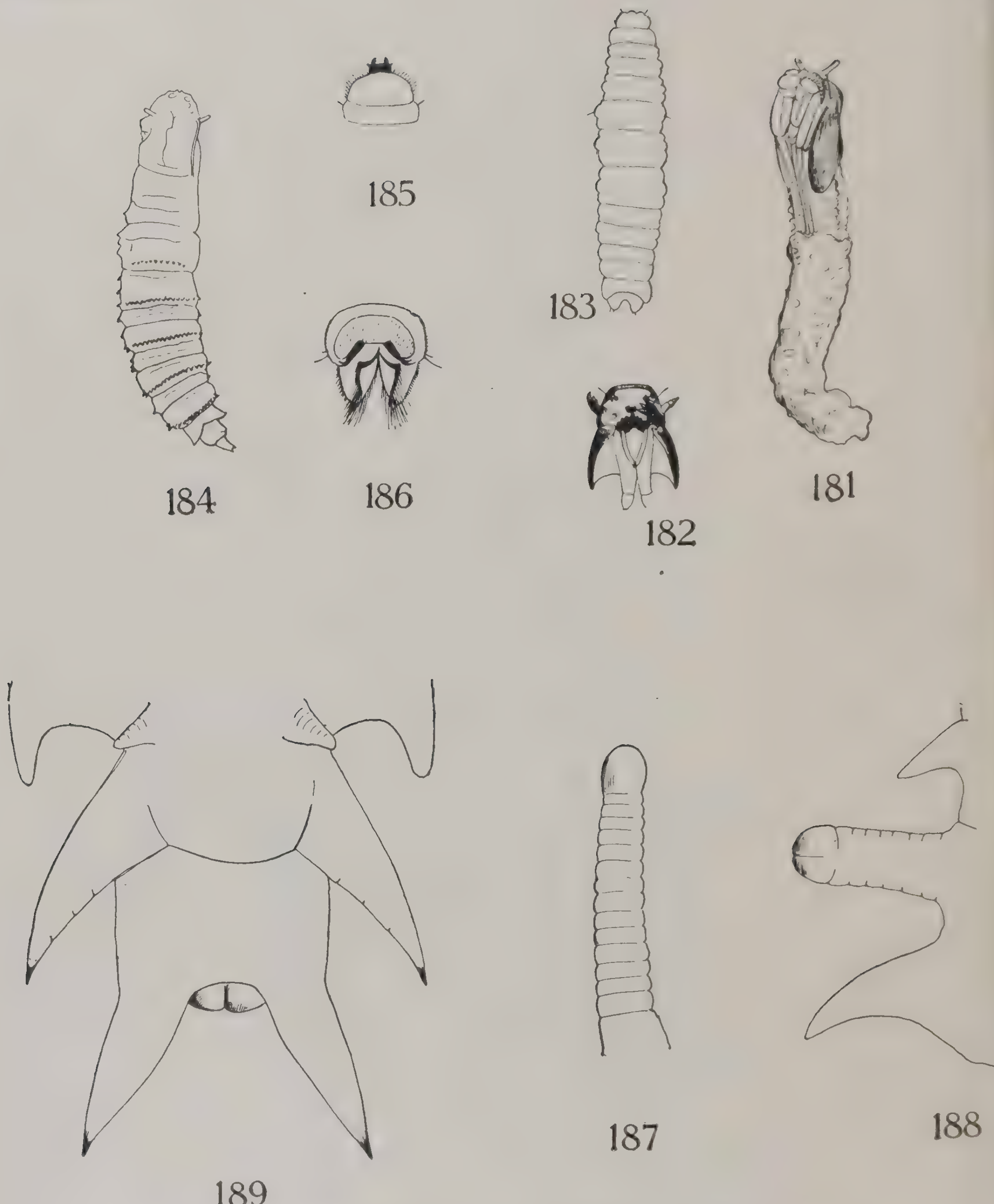
Pseudolimnophila luteipennis, larva: 172, mentum; 173, hypopharynx; 175, mandible; 176, spiracular disk
Pseudolimnophila inornata, larva: 174, antenna



PSEUDOLIMNOPHILA INORNATA AND P. LUTEIPENNIS

Pseudolimnophila inornata, pupa: 177, pronotal breathing horn

Pseudolimnophila luteipennis, pupa: 178, male cauda, lateral aspect; 179, female cauda, dorsal aspect; 180, female cauda, ventral aspect



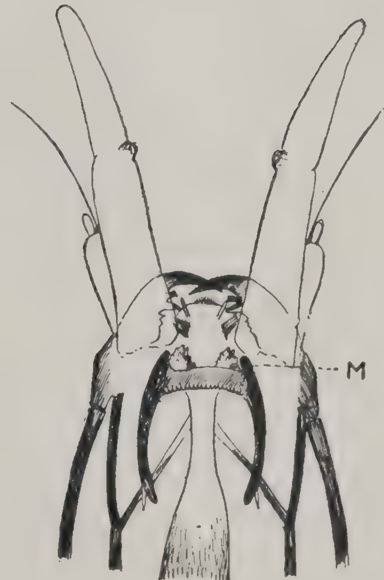
DACTYLOLABIS DENTICULATA, D. WODZICKII, AND D. CUBITALIS

Dactylolabis denticulata (after Mik): 181, pupa; 182, larva, head capsule, ventral aspect; 183, larva, dorsal aspect

Dactylolabis wodzickii (after Nowicki): 184, pupa; 185, larva, head capsule; 186, larva, spiracular disk

Dactylolabis cubitalis, pupa: 187, pronotal breathing horn; 188, second abdominal segment, showing spiracle; 189, male cauda, dorsal aspect

190



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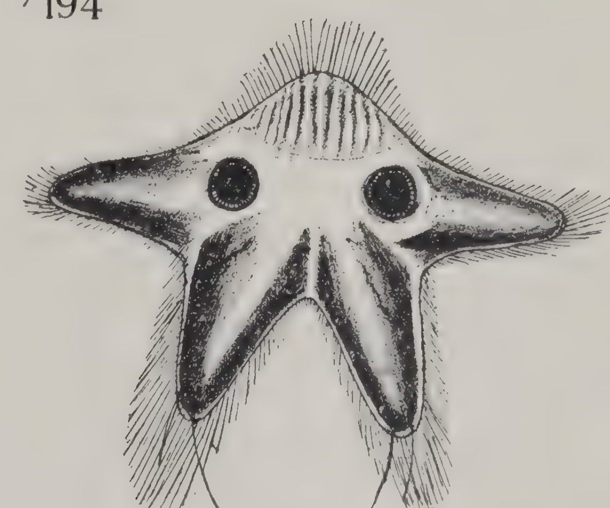
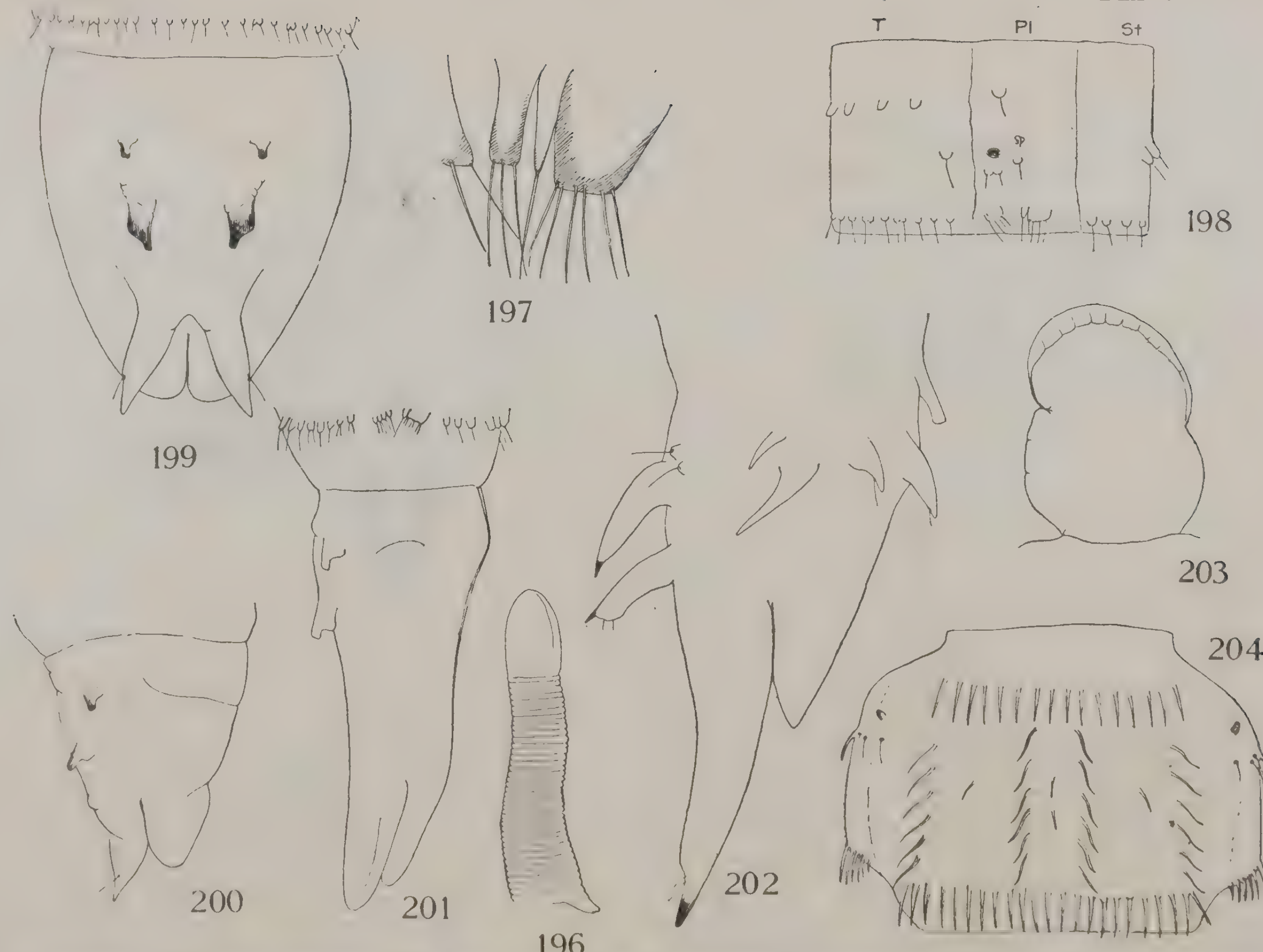


195

LIMNOPHILA (DICRANOPHRAGMA) FUSCOVARIA, LARVA

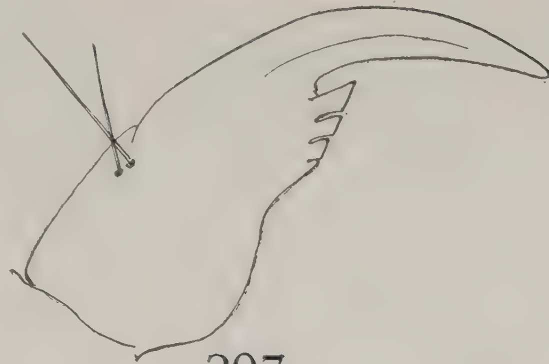
190, Cephalic and caudal ends, dorsal aspect; 191, head capsule, ventral aspect; 192, labrum epipharynx; 193, antenna; 194, mandible; 195, spiracular disk



LIMNOPHILA (DICRANOPHRAGMA) FUSCOVARIA AND LIMNOPHILA (PHYLIDOREA) ADUSTA, SUPPOSITION

Limnophila (*Dicranophragma*) *fuscovaria*, pupa: 196, pronotal breathing horn; 197, pleural abdominal spines; 198, fifth abdominal segment (diagrammatic); 199, male cauda, dorsal aspect; 200, male cauda, lateral aspect; 201, female cauda, lateral aspect

Limnophila (*Phylidorea*) *adusta* (supp.), pupa: 202, female cauda, lateral aspect; 203, pronotal breathing horn; 204, fifth abdominal segment, ventral aspect



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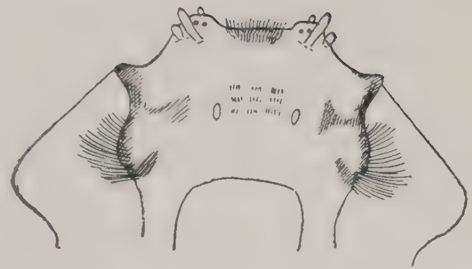

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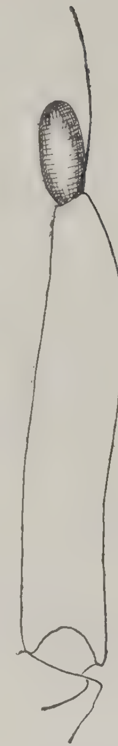

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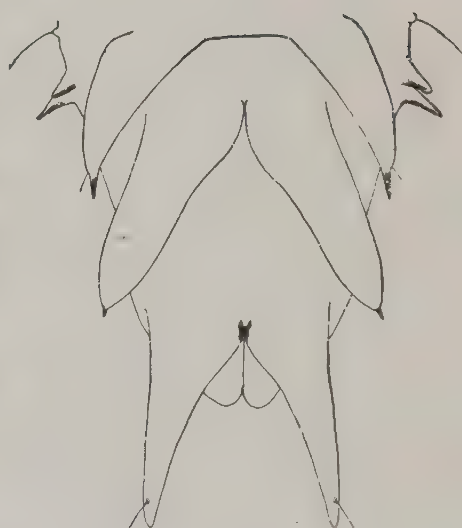
LIMNOPHILA (LASIOMASTIX) MACROCERA, LARVA

205, Labrum; 206, antenna; 207, mandible; 208, spiracular disk, dorsal aspect

210



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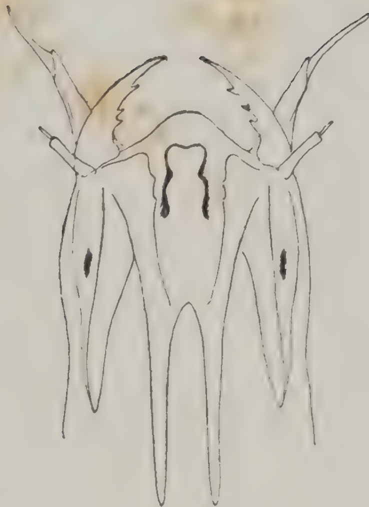
LIMNOPHILA (LASIOMASTIX) MACROCERA, PUPA

209, Male, lateral aspect; 210, mouth parts; 211, male cauda, dorsal aspect; 212, female cauda, lateral aspect



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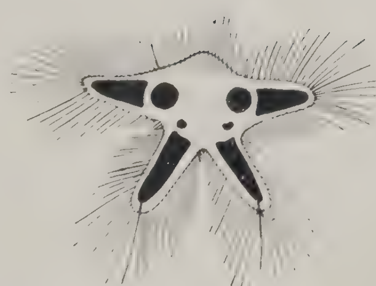

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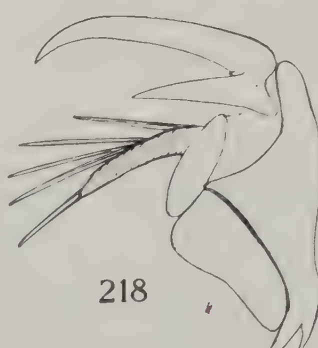

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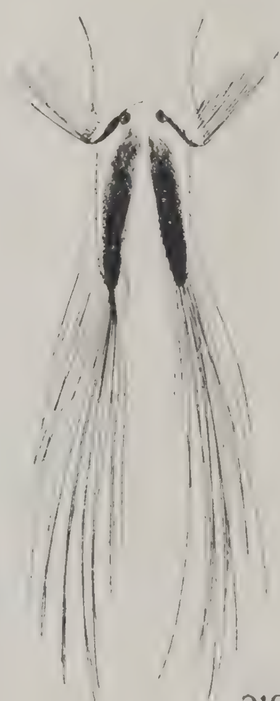

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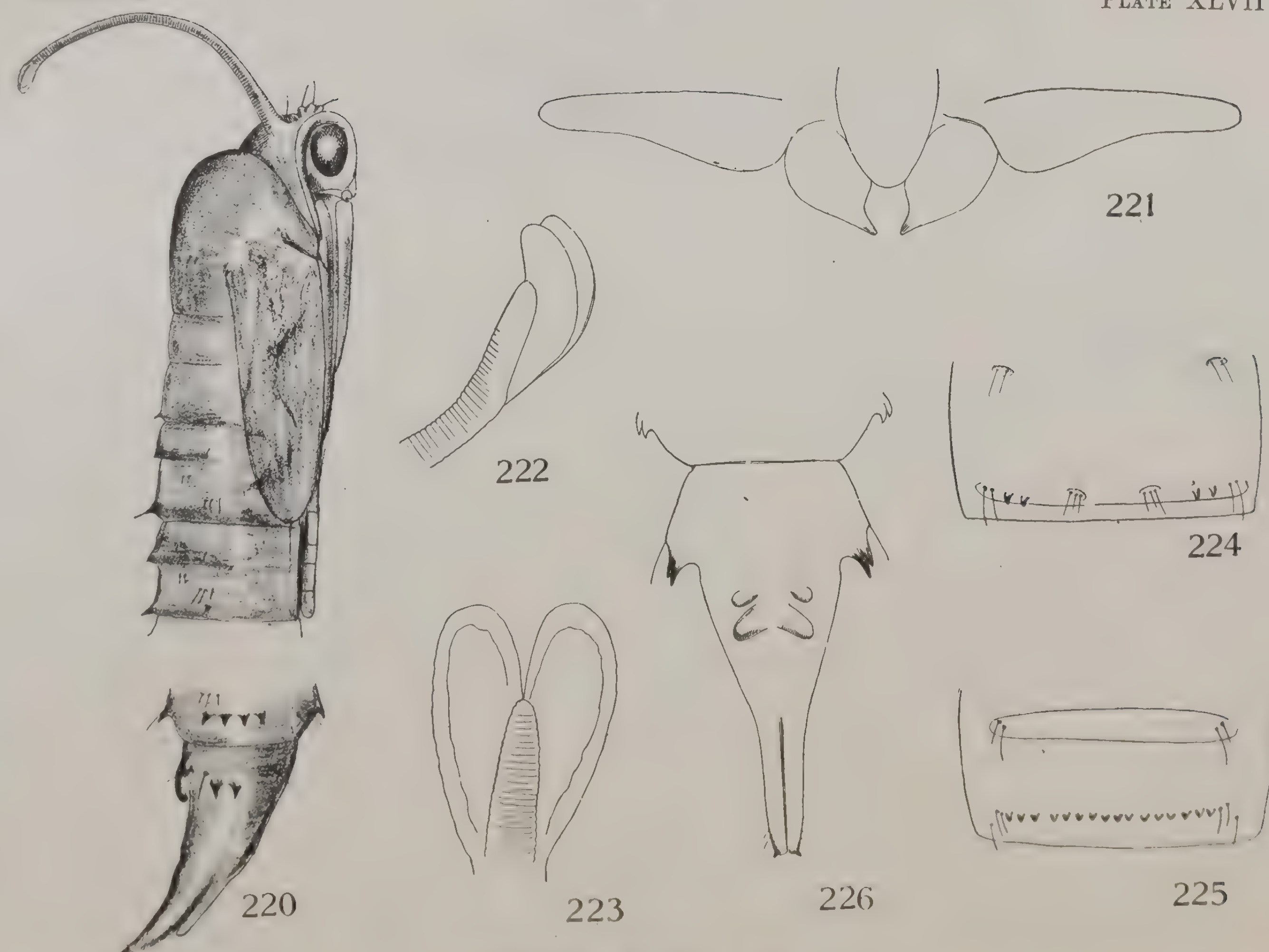
LIMNOPHILA PICTIPENNIS, L. PUNCTATA, AND ULOMORPHA PILOSELLA

Limnophila pictipennis: 213, head capsule (after Brauer)
Limnophila punctata: 214, spiracular disk (after Gerbig)
Ulomorpha pilosella, larva: 215, head capsule, dorsal aspect; 216, labrum; 217, antenna; 218, mandible; 219, spiracular disk, dorsal aspect



ULOMORPHA PILOSELLA, PUPA

220, Female, lateral aspect; 221, mouth parts; 222, apex of breathing horn; 223, apex of breathing horn viewed from beneath; 224, fifth abdominal segment, dorsal aspect; 225, fifth abdominal segment, ventral aspect; 226, female cauda, dorsal aspect

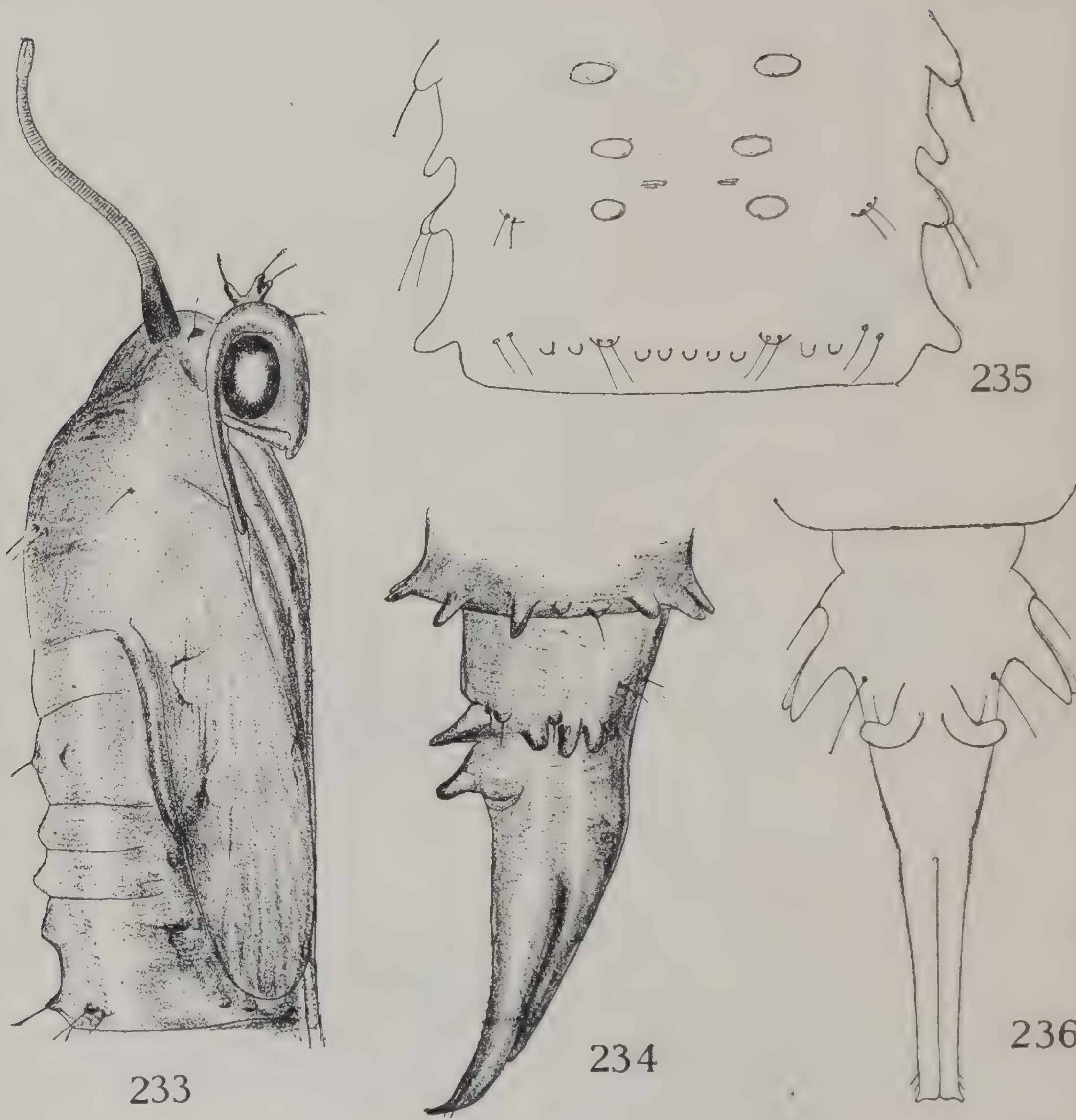
227 228

229

230 231 232

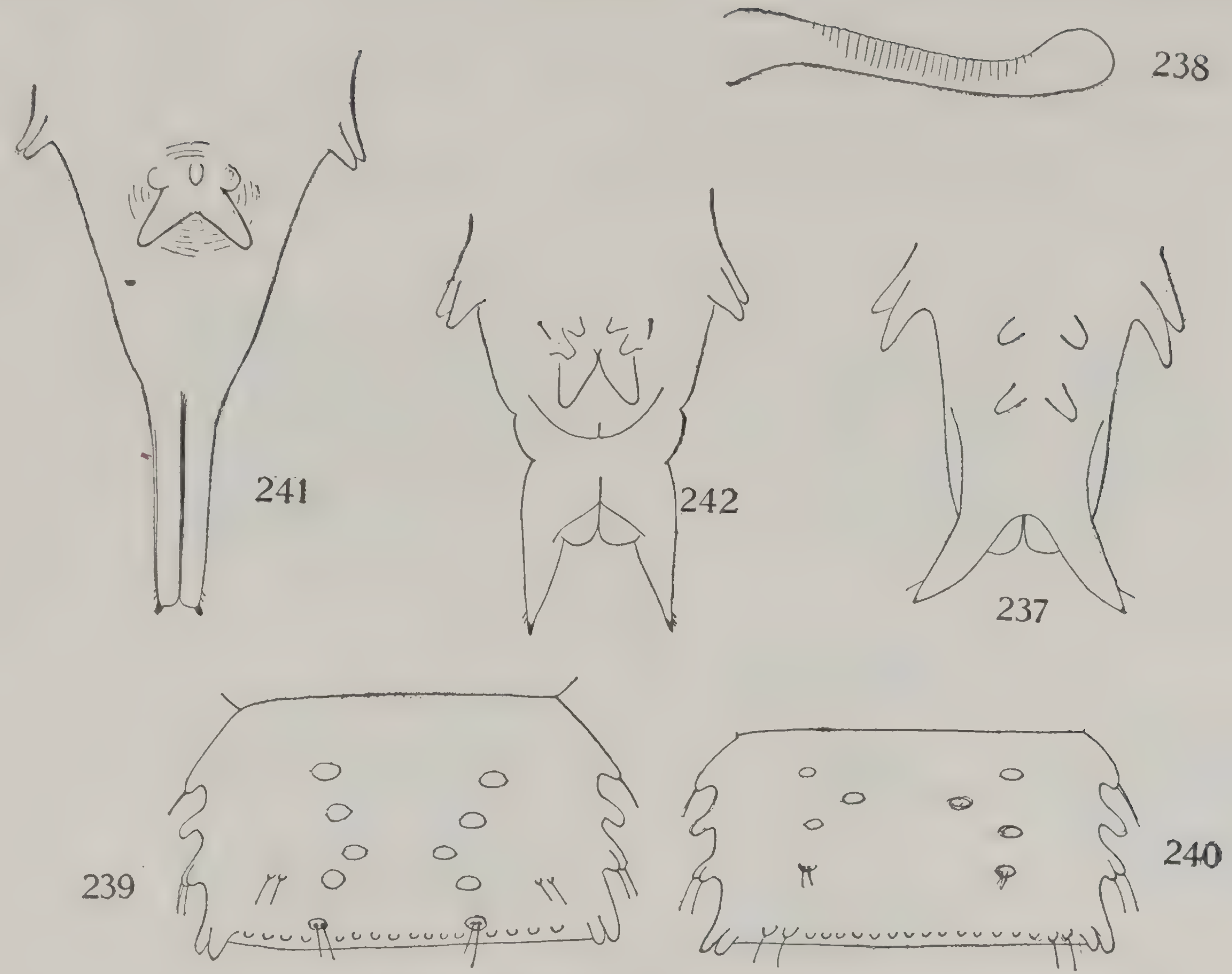
PILARIA RECONDITA, P. TENUIPES, P. FUSCIPENNIS, AND P. DISCICOLLIS

Pilaria recondita, larva: 227, tip of mandible
Pilaria tenuipes, larva: 228, tip of mandible; 229, antenna; 230, spiracular disk, dorsal aspect
Pilaria fuscipennis: 231, spiracular disk (after Gerbig)
Pilaria discicollis: 232, spiracular disk (after Gerbig)



PILARIA TENUIPES, PUPA

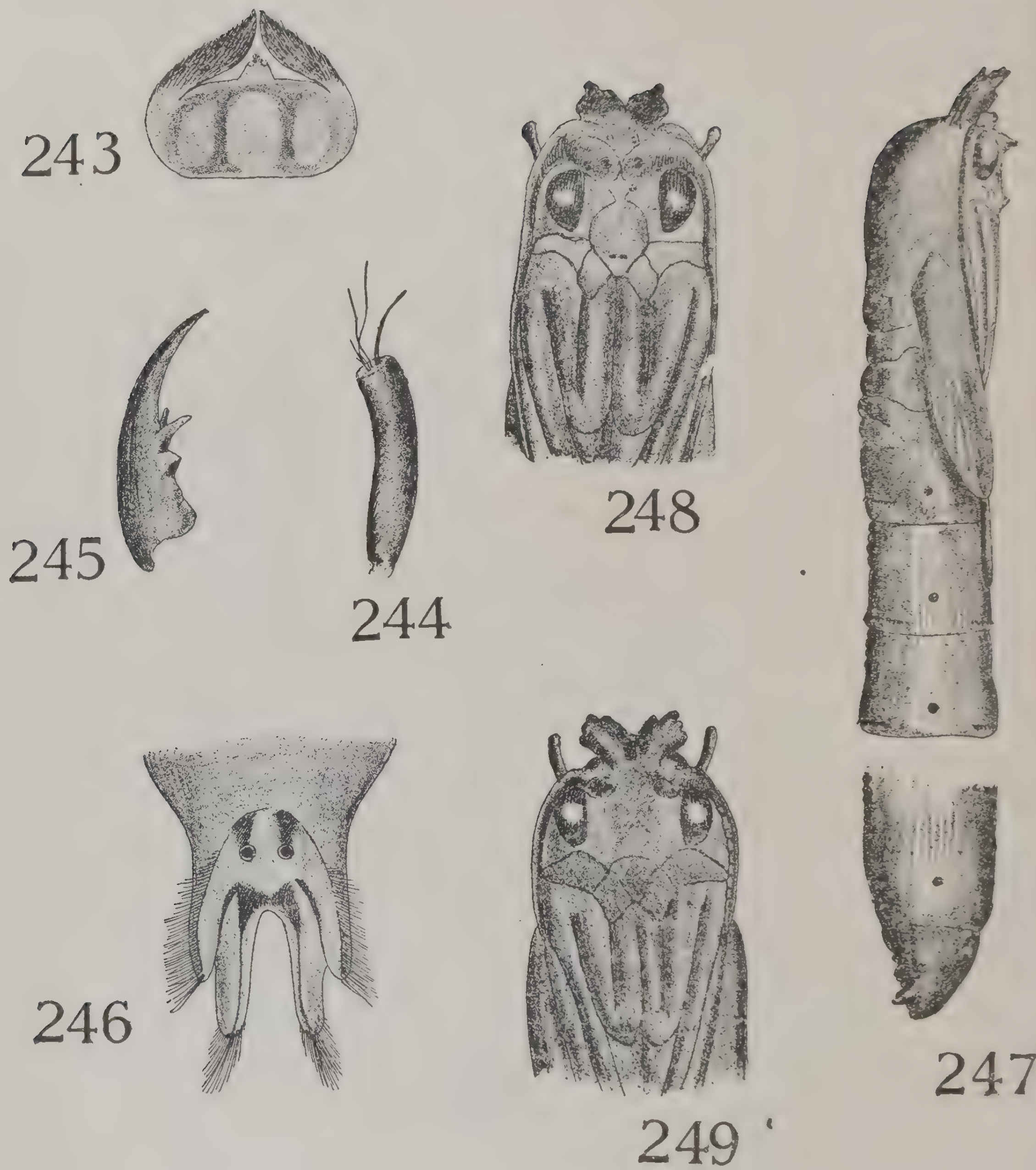
233, Female, lateral aspect; 234, female cauda, lateral aspect; 235, fifth abdominal segment, dorsal aspect; 236, female cauda, dorsal aspect



PILARIA RECONDITA AND P. QUADRATA

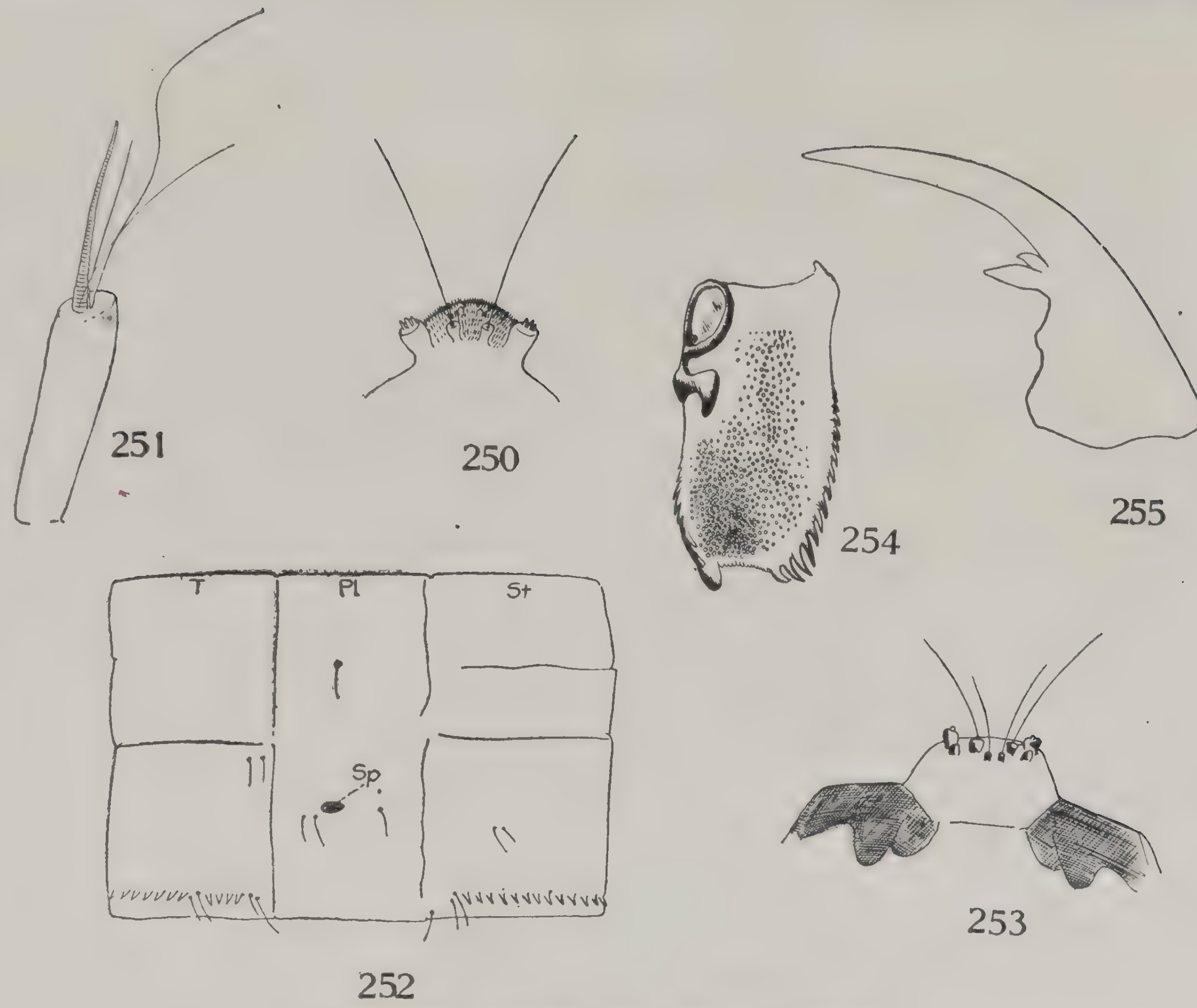
Pilaria recondita, pupa: 237, male cauda, dorsal aspect

Pilaria quadrata, pupa: 238, pronotal breathing horn; 239, fifth abdominal segment, dorsal aspect; 240, fifth abdominal segment, ventral aspect; 241, female cauda, dorsal aspect; 242, male cauda, dorsal aspect



HEXATOMA MEGACERA

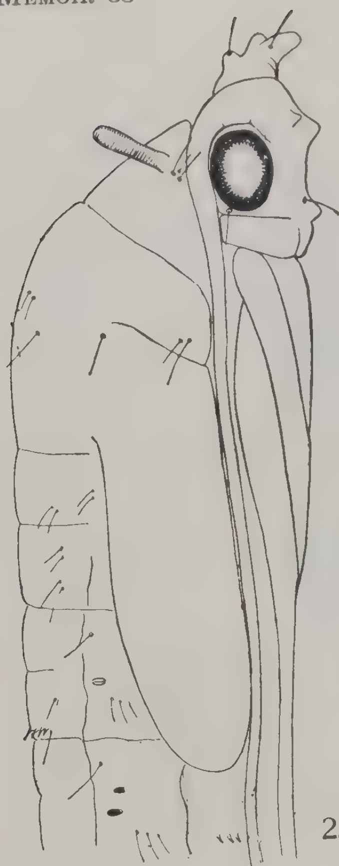
Larva: 243, labrum; 244, antenna; 245, mandible; 246, spiracular disk
Pupa: 247, lateral aspect; 248, male, ventral aspect; 249, female, ventral aspect



HEXATOMA MEGACERA AND ERIOCERA CINEREA

Hexatoma megacera: 250, larva, apex of labrum; 251, larva, antenna; 252, pupa, fifth abdominal segment, lateral aspect

Eriocera cinerea, larva: 253, labrum; 254, pharyngeal plate; 255, mandible



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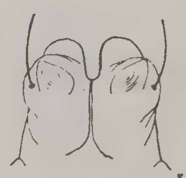

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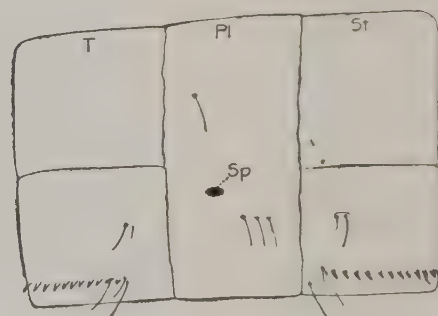

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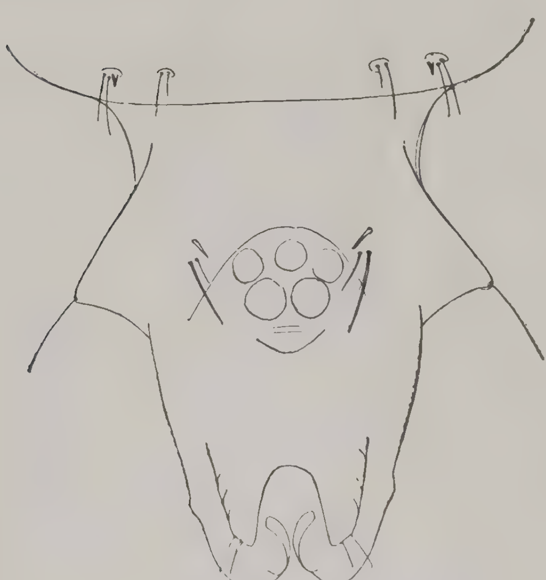

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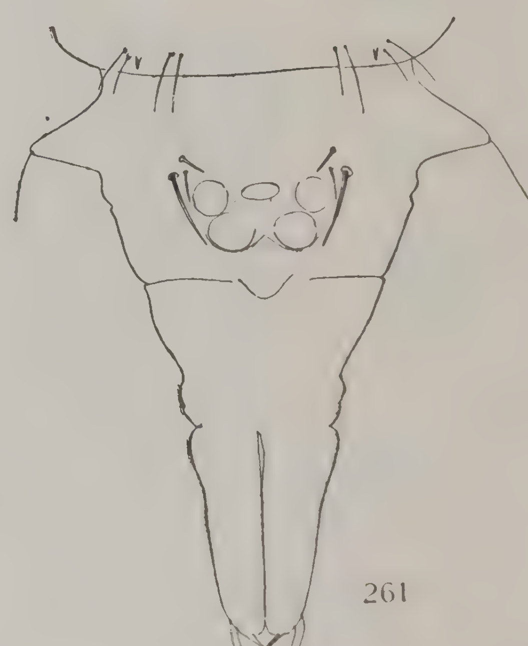

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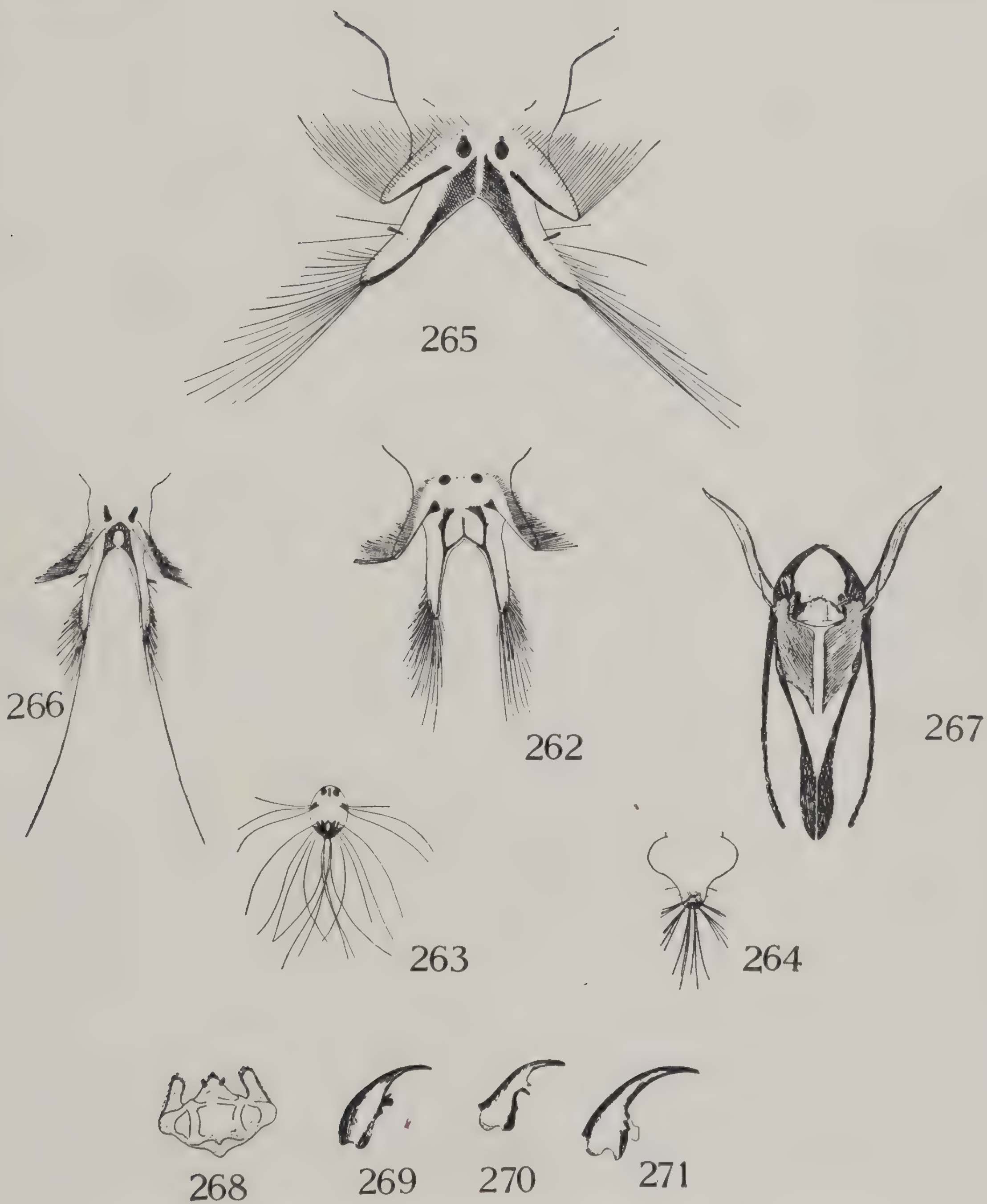
ERIOCERA CINEREA, PUPA

256, Male, lateral aspect; 257, cephalic crest of male, ventral aspect; 258, mouth parts; 259, fifth abdominal segment, lateral aspect; 260, male cauda, dorsal aspect; 261, female cauda, dorsal aspect



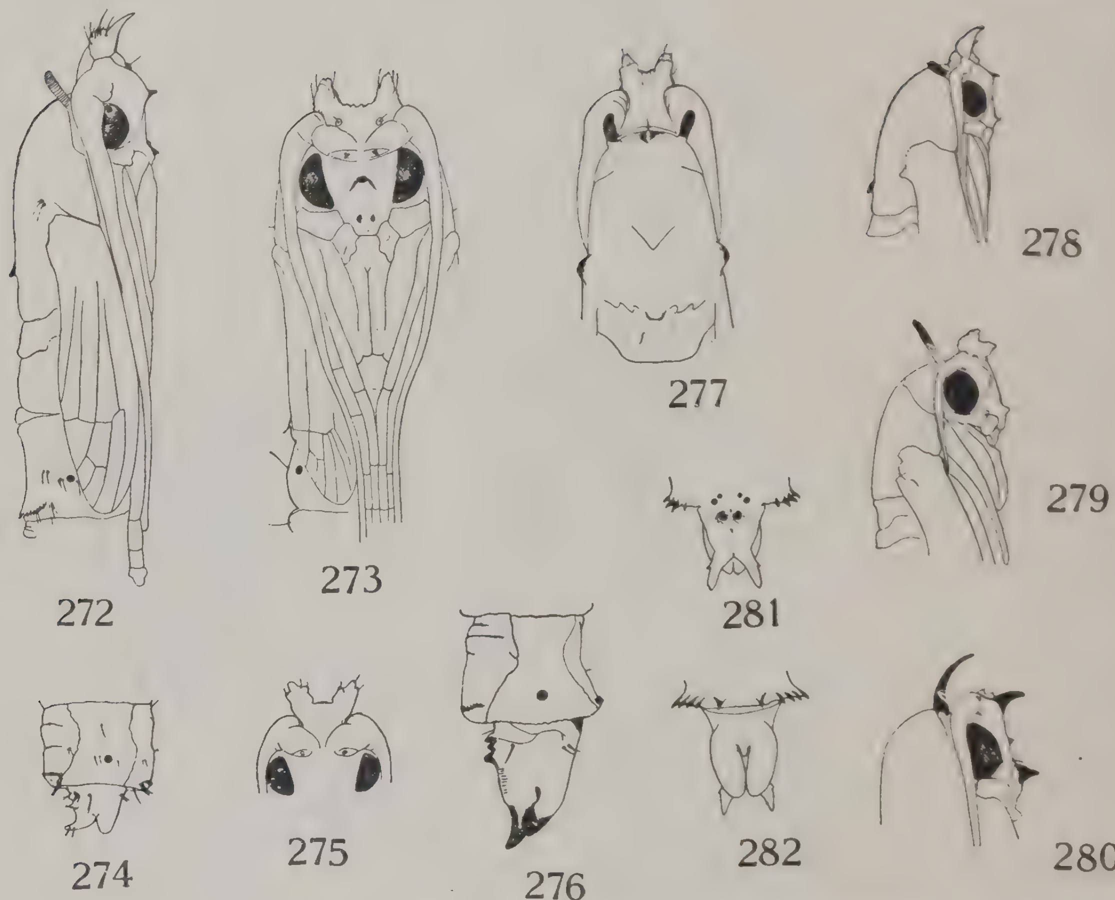
ERIOCERA SPINOSA, E. CINEREA, E. LONGICORNIS, AND E. FULTONENSIS

Eriocera spinosa, larva: 262, spiracular disk; 267, head capsule, dorsal aspect; 271, mandible

Eriocera cinerea, larva: 263 and 264, spiracular disk; 270, mandible

Eriocera longicornis, larva: 265, spiracular disk

Eriocera fultonensis, larva: 266, spiracular disk; 268, labrum; 269, mandible

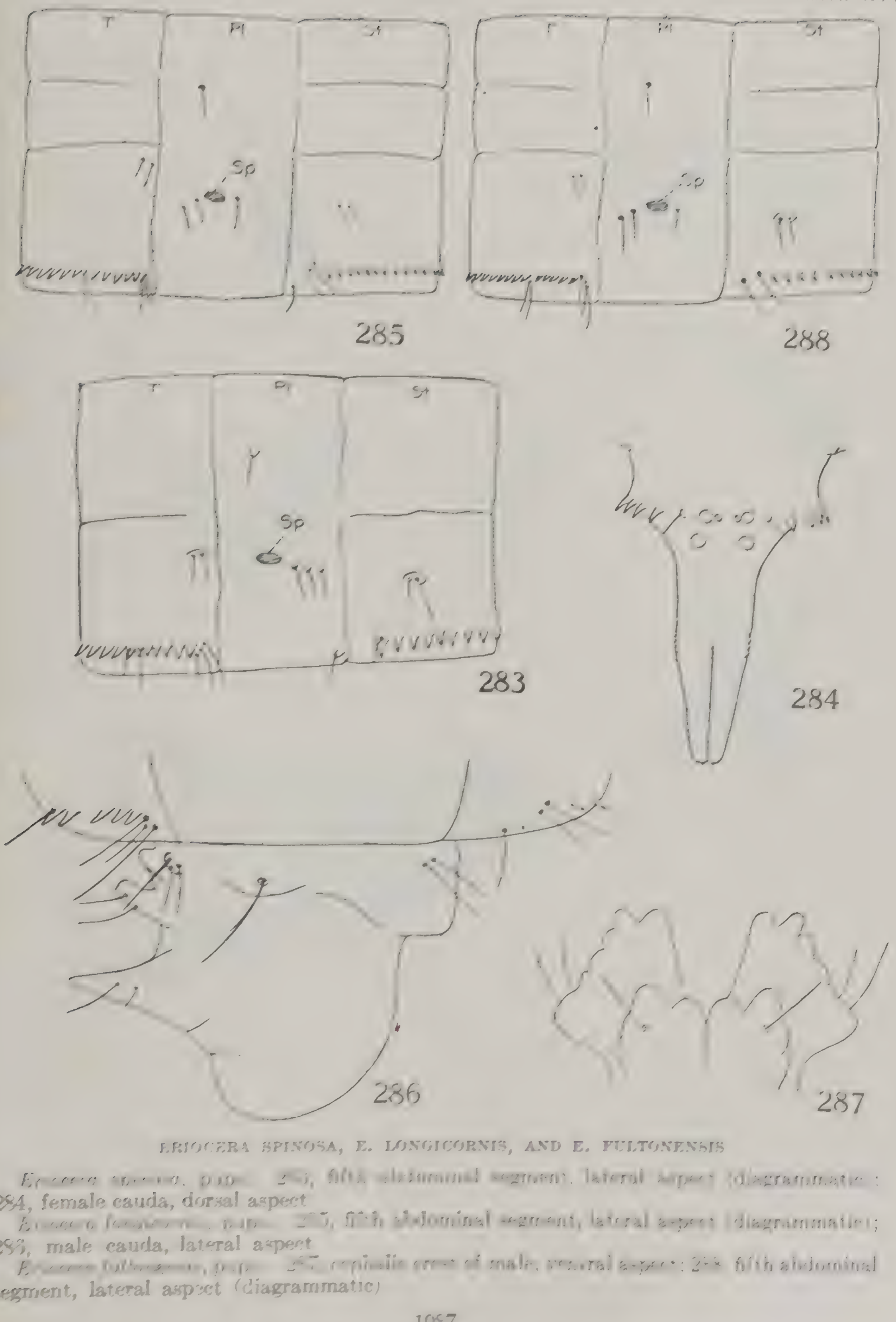


ERIOCERA LONGICORNIS, E. FULTONENSIS, AND E. SPINOSA

Eriocera longicornis, pupa: 272, male, lateral aspect; 273, male, ventral aspect; 274, female cauda, lateral aspect; 275, head of male, ventral aspect; 277, thorax of male, dorsal aspect; 278, female, lateral aspect

Eriocera fultonensis, pupa: 276, female cauda, lateral aspect; 279, female, lateral aspect

Eriocera spinosa, pupa: 280, female, lateral aspect; 281, male cauda, dorsal aspect; 282, male cauda, ventral aspect

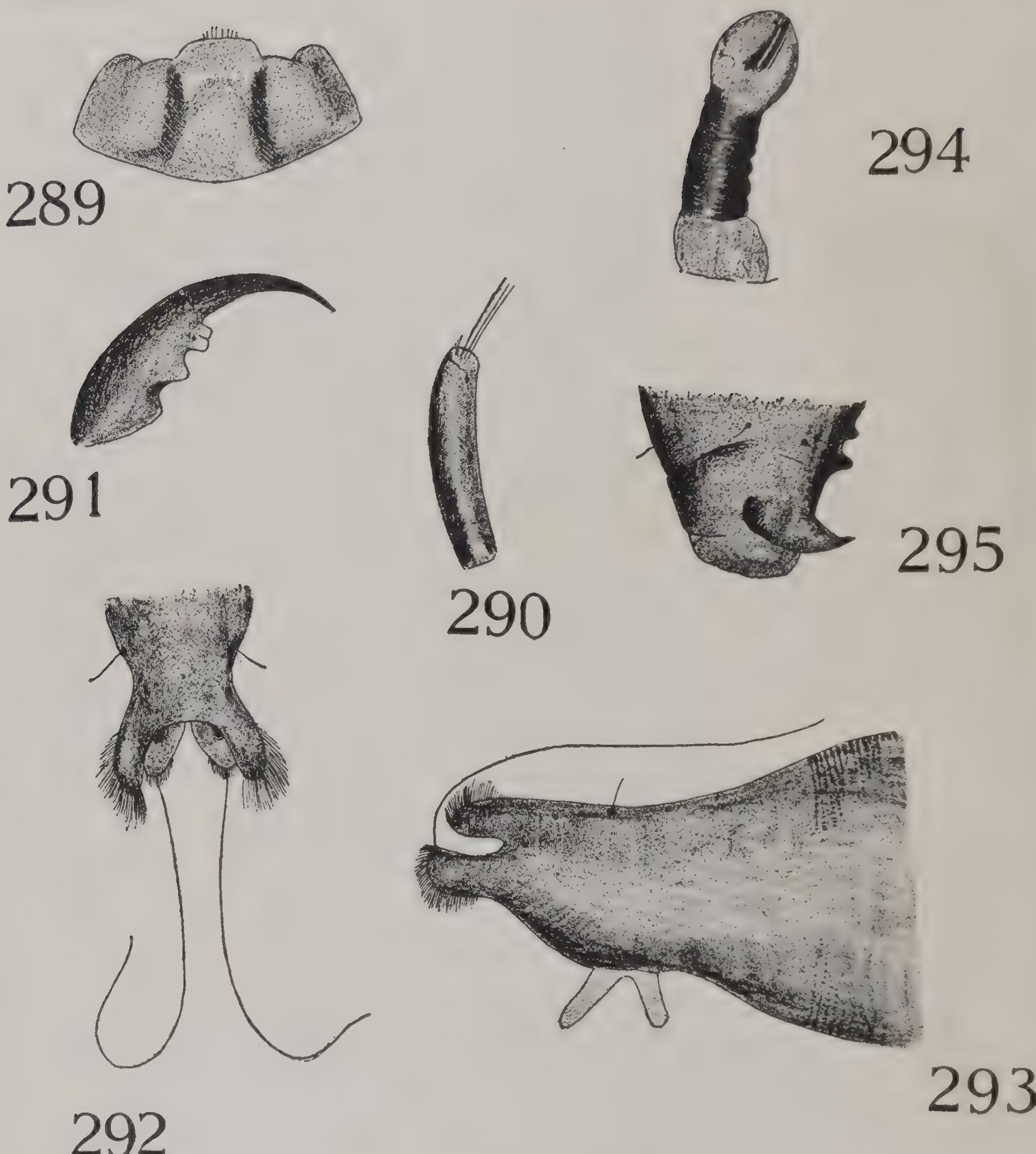


ERIOCERA SPINOSA, E. LONGICORNIS, AND E. FULTONENSIS

Eriocera spinosa, pupa: 283, fifth abdominal segment, lateral aspect (diagrammatic); 284, female cauda, dorsal aspect

Eriocera longicornis, pupa: 285, fifth abdominal segment, lateral aspect (diagrammatic); 286, male cauda, lateral aspect

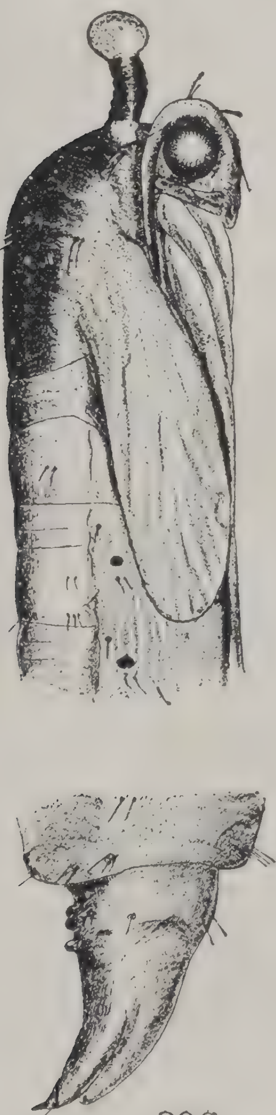
Eriocera fultonensis, pupa: 287, cephalic crest of male, ventral aspect; 288, fifth abdominal segment, lateral aspect (diagrammatic)



PENTHOPTERA ALBITARSIS

Larva: 289, labrum; 290, antenna; 291, mandible; 292, spiracular disk, dorsal aspect; 293, spiracular disk, lateral aspect

Pupa: 294, pronotal breathing horn; 295, male cauda, lateral aspect



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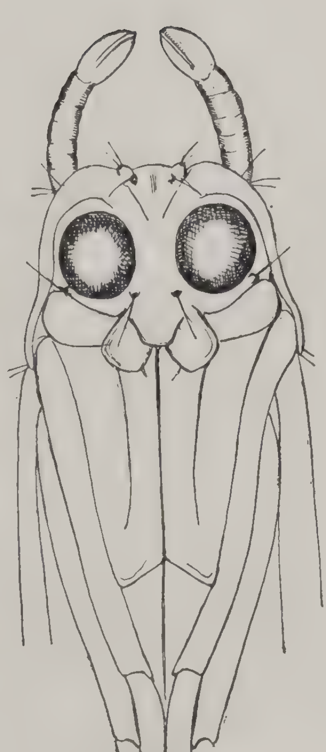

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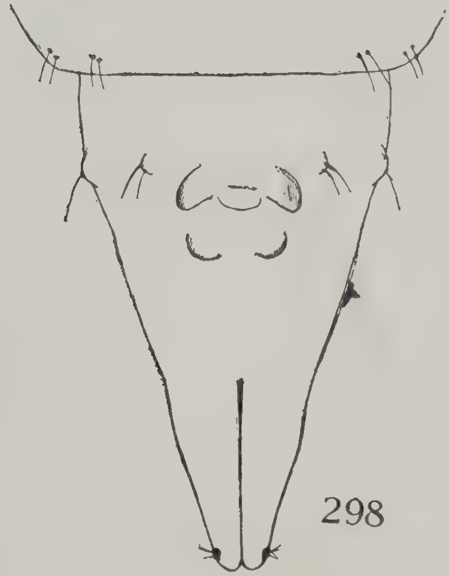

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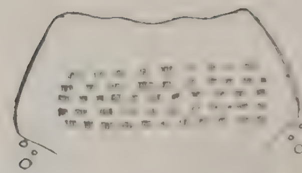
PENTHOPTERA ALBITARSIS, PUPA

296, Female, lateral aspect; 297, female, ventral aspect; 298, female cauda, dorsal aspect; 299, male cauda, lateral aspect



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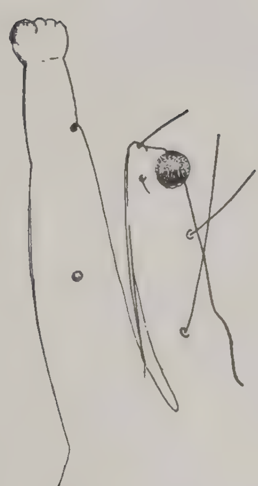

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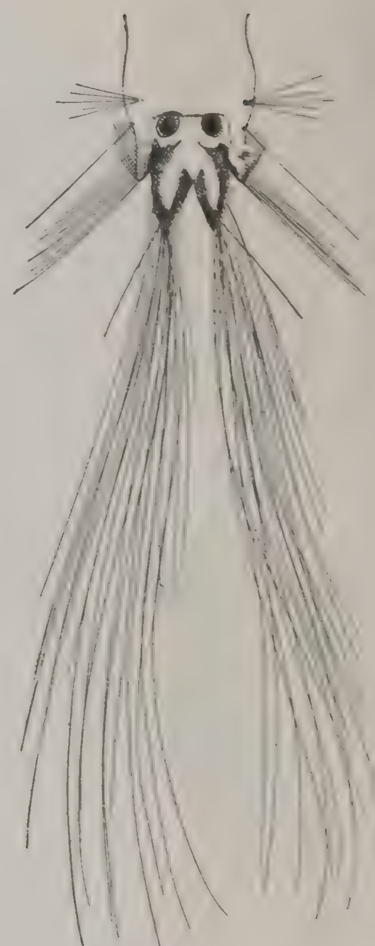
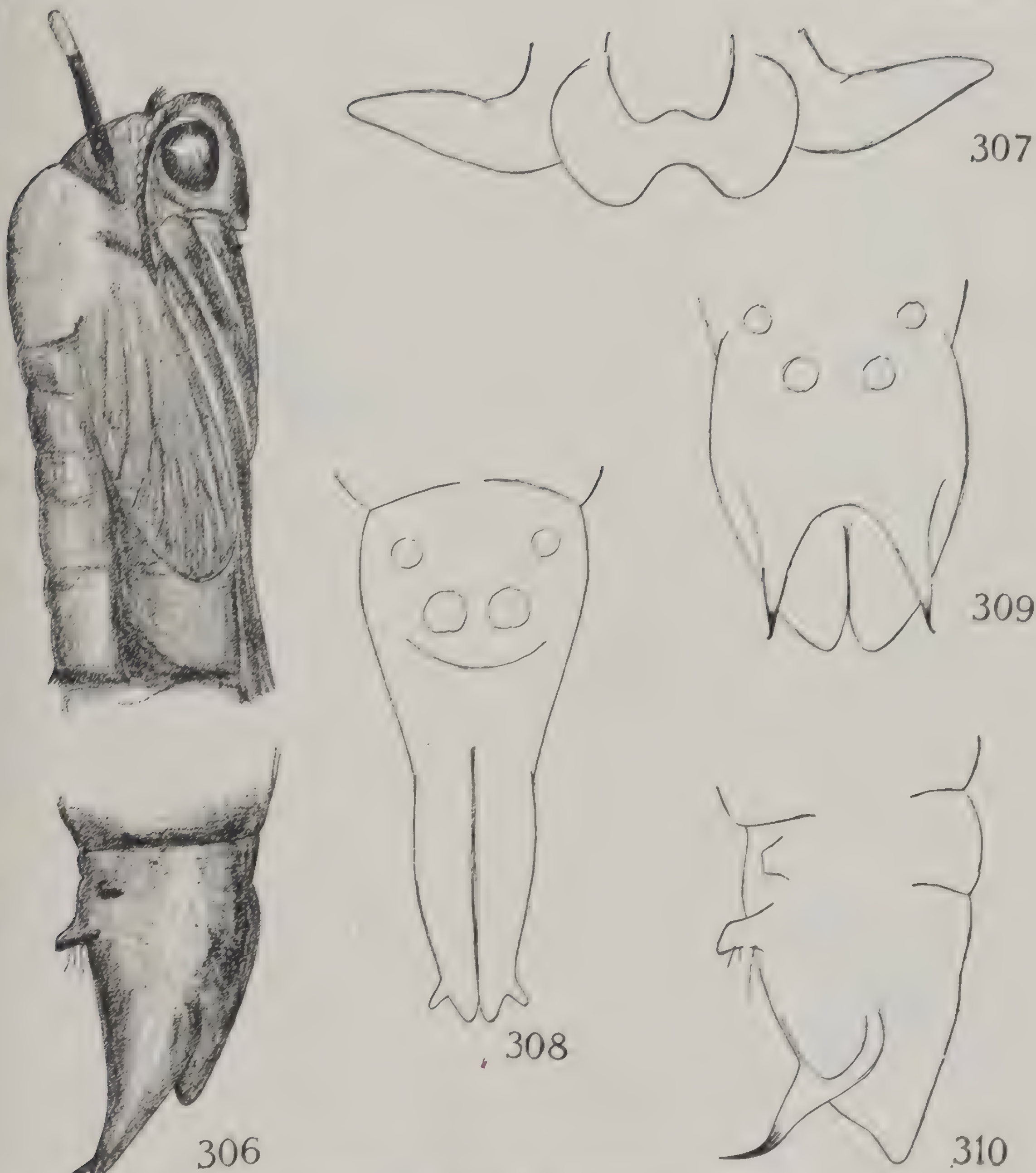


305

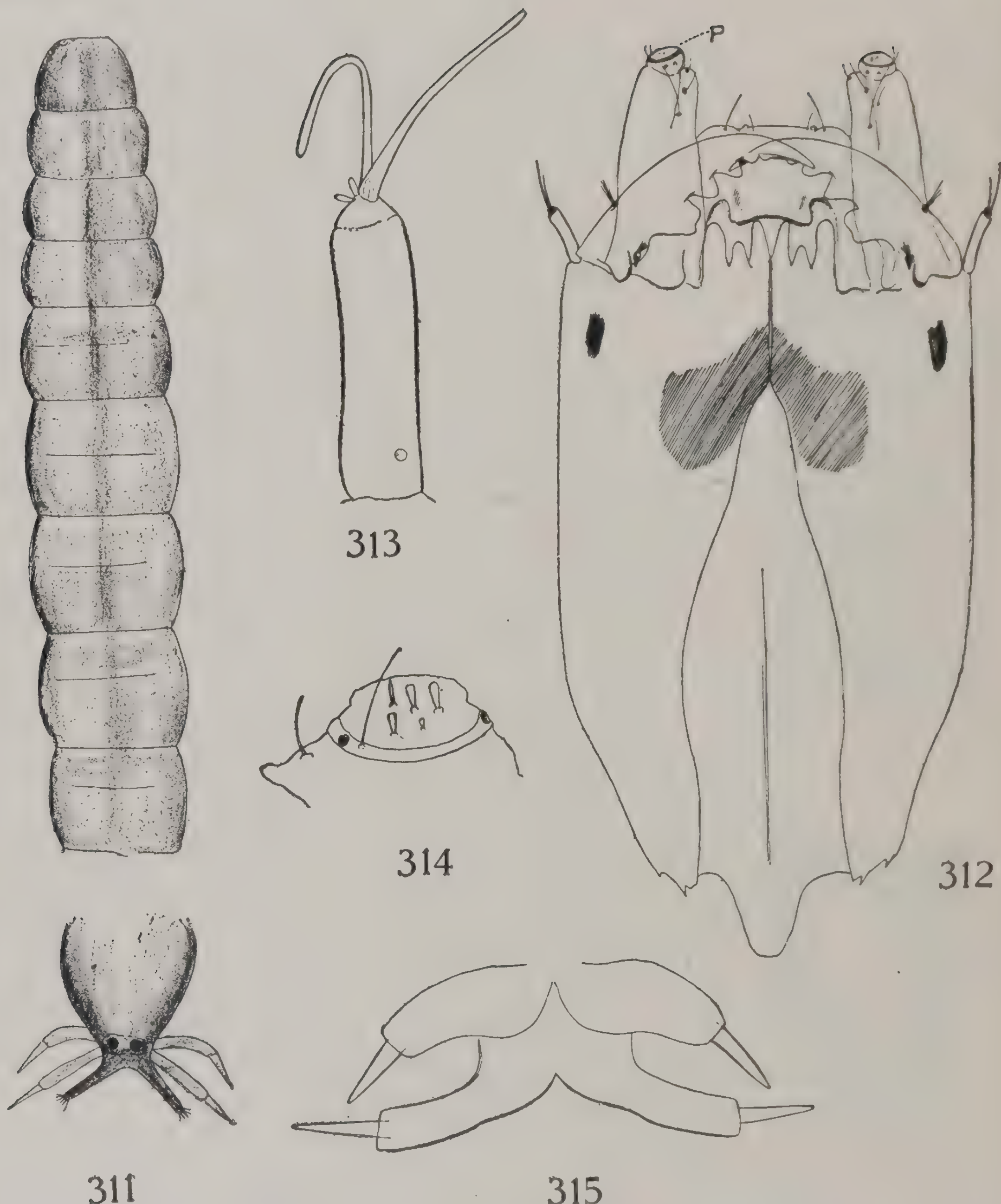
ADELPHOMYIA MINUTA (SUPPOSITION), LARVA

300, Labrum; 301, antenna; 302, mentum; 303, mandible; 304, maxilla; 305, spiracular disk



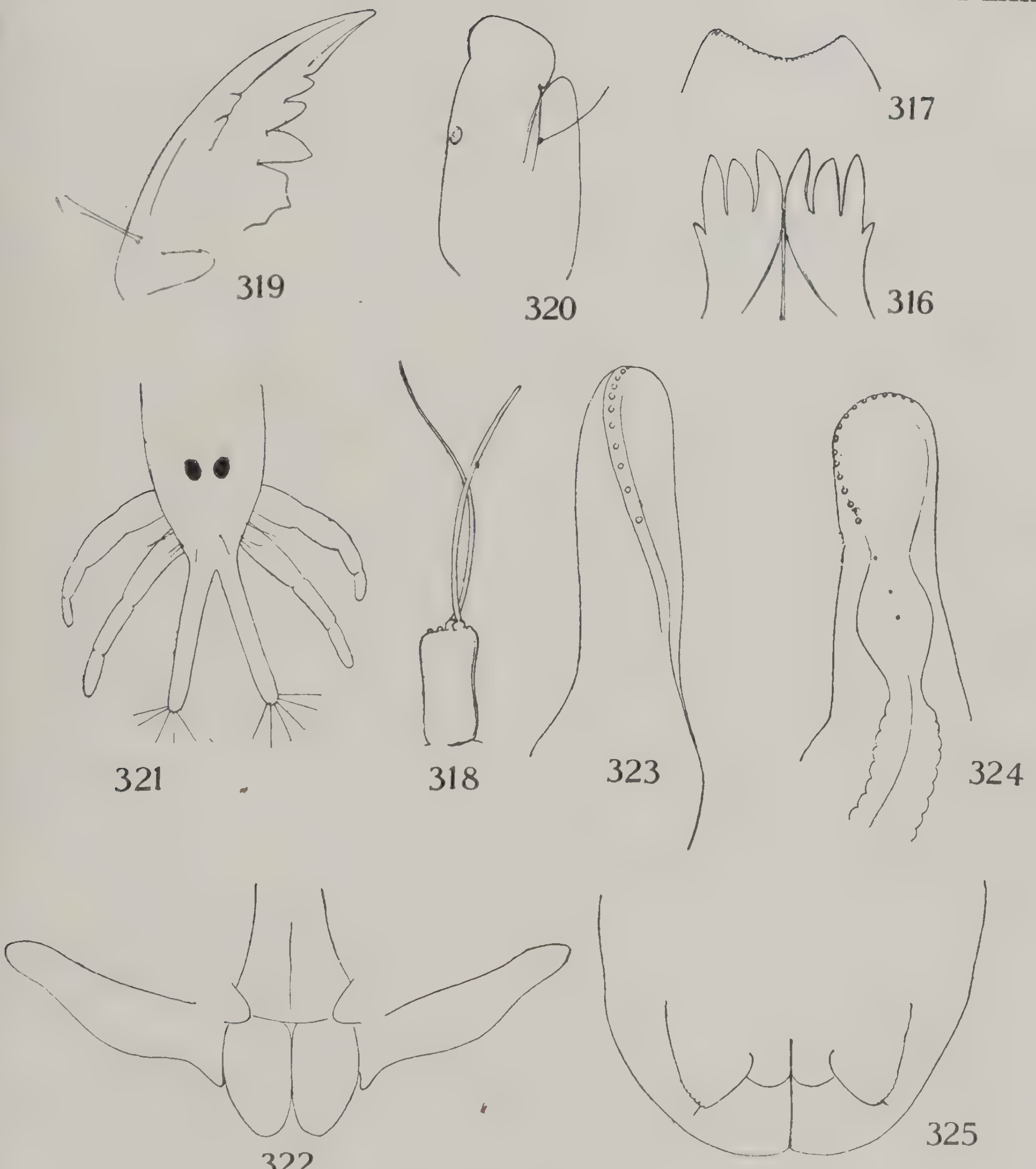
ADELPHOMYIA MINUTA (SUPPOSITION), PUPA

306, Female, lateral aspect; 307, mouth parts; 308, female cauda, dorsal aspect; 309, male cauda, dorsal aspect; 310, male cauda, lateral aspect



PEDICIA ALBIVITTA, LARVA

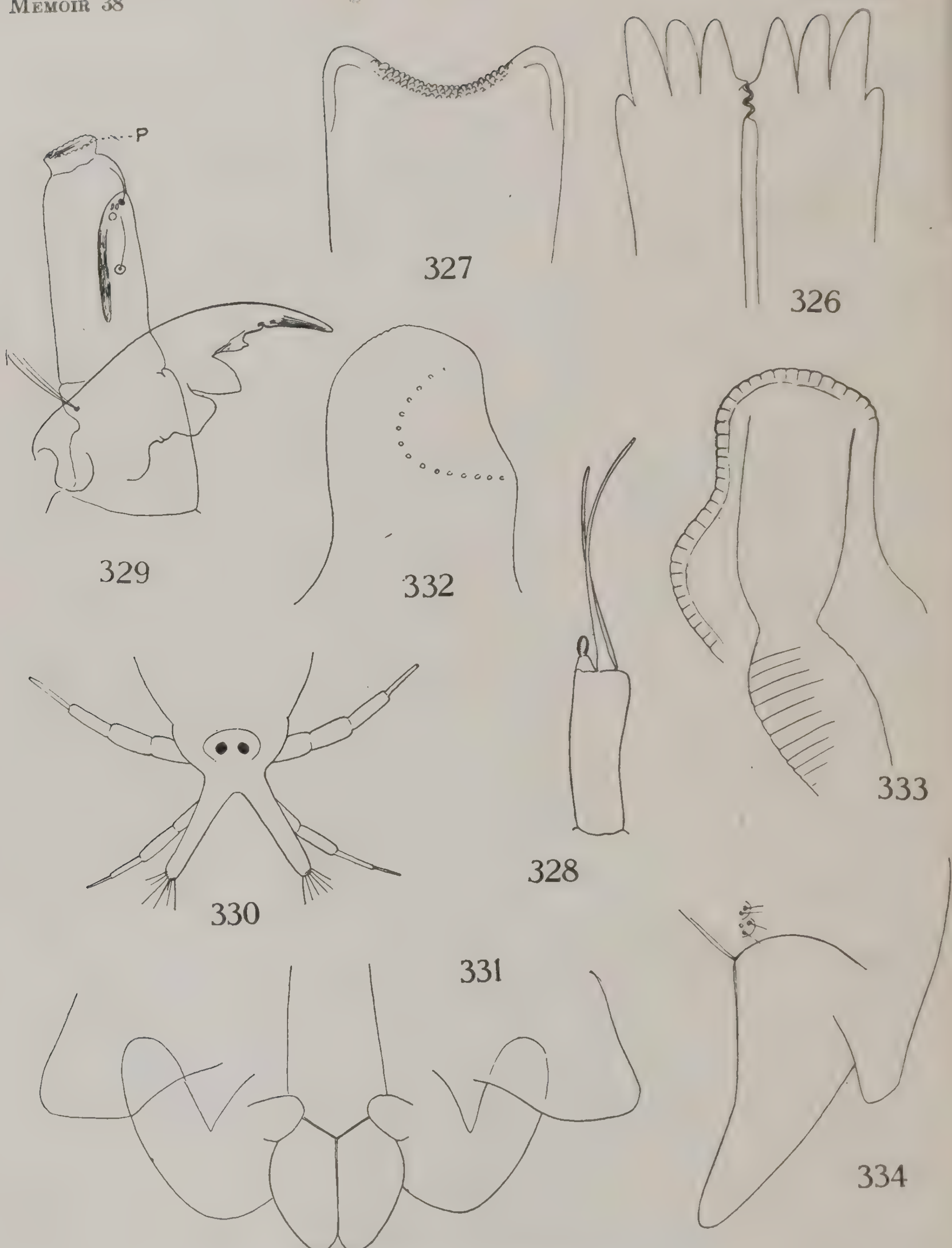
311, Dorsal aspect; 312, head capsule, ventral aspect; 313, antenna; 314, maxillary palpus; 315, anal gills, ventral aspect



RHAPHIDOLABINA FLAVEOLA

Larva: 316, mentum; 317, hypopharynx; 318, antenna; 319, mandible; 320, maxilla; 321, spiracular disk

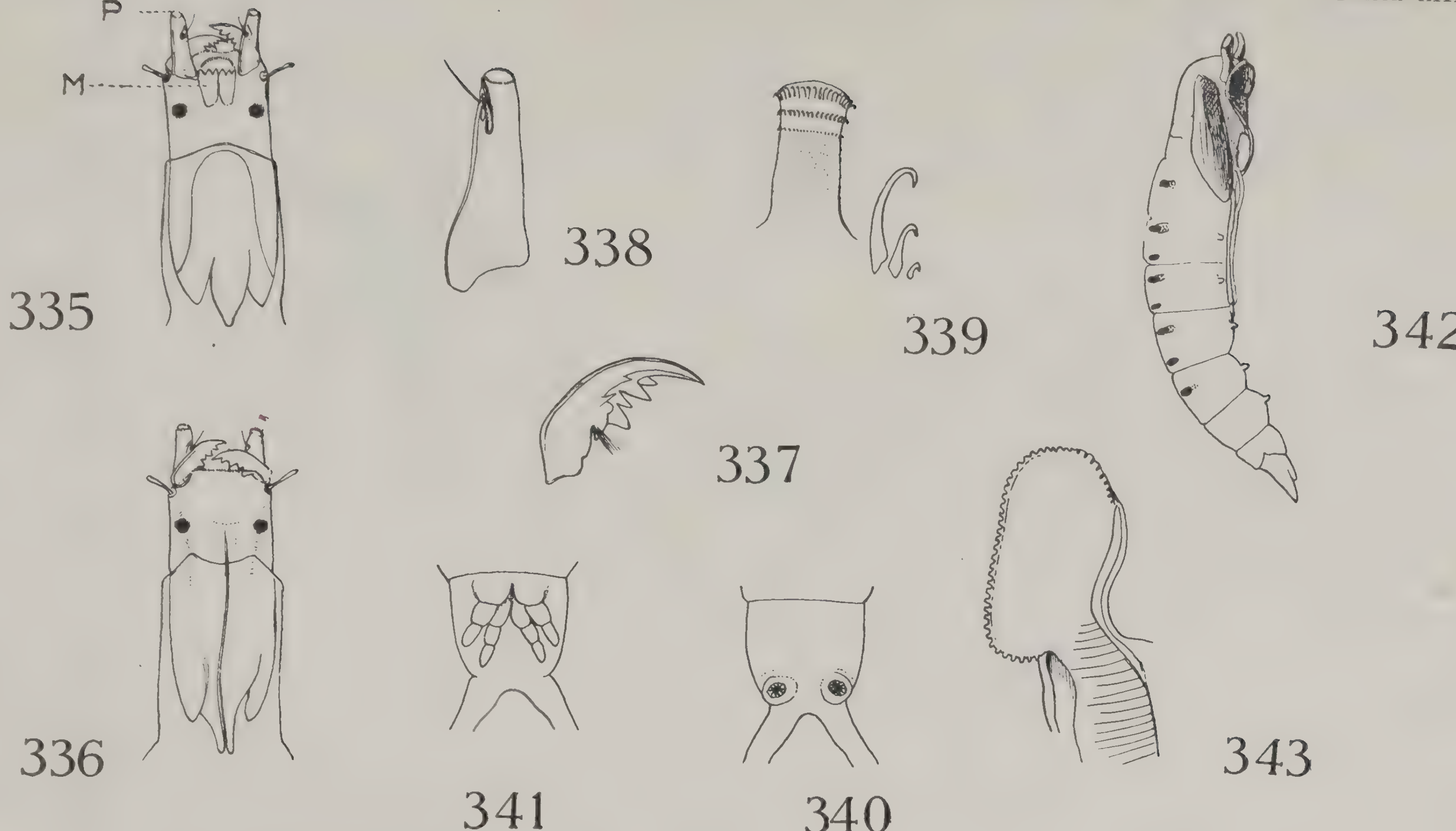
Pupa: 322, mouth parts; 323, pronotal breathing horn, dorsal aspect; 324, pronotal breathing horn, lateral aspect; 325, male cauda, dorsal aspect



TRICYPHONA INCONSTANS

Larva: 326, mentum; 327, hypopharynx; 328, antenna; 329, mandible and maxilla; 330, spiracular disk

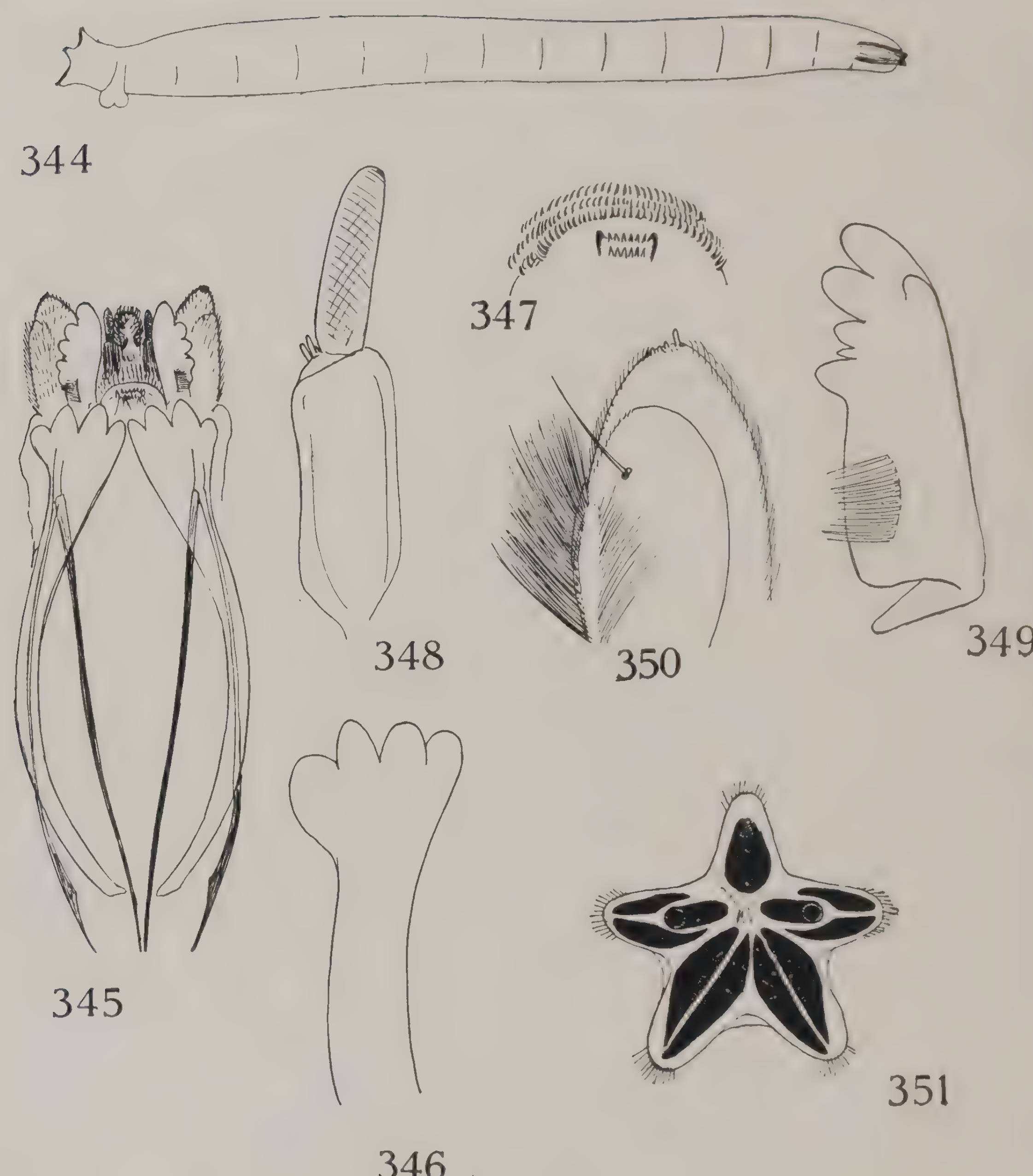
Pupa: 331, mouth parts; 332, pronotal breathing horn, dorsal aspect; 333, pronotal breathing horn, lateral aspect; 334, female cauda, lateral aspect



DICRANOTA BIMACULATA (AFTER MIALL)

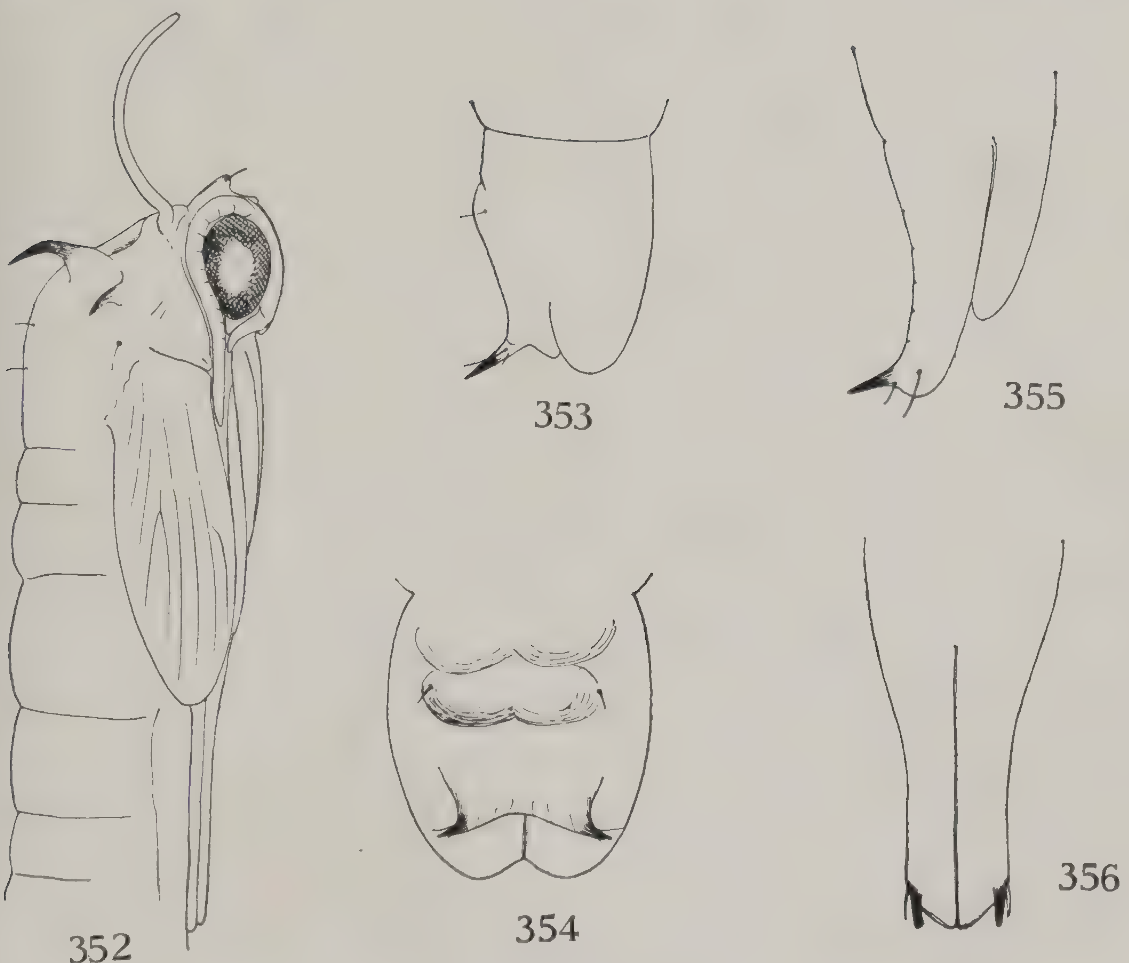
Larva: 335, head capsule, ventral aspect; 336, head capsule, dorsal aspect; 337, mandible; 338, maxillary palpus; 339, abdominal pseudopods; 340, spiracular disk, dorsal aspect; 341, anal gills

Pupa: 342, female, lateral aspect; 343, pronotal breathing horn



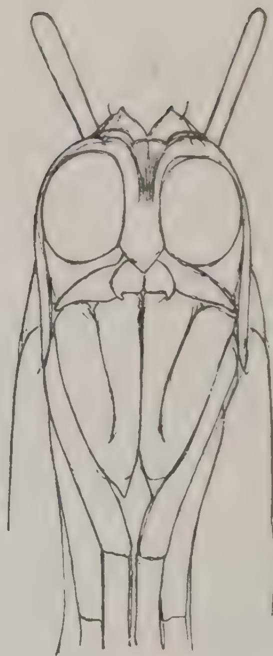
MOLOPHILUS HIRTIPENNIS, LARVA

344, Lateral aspect; 345, head capsule, ventral aspect; 346, mental plate; 347, hypopharynx; 348, antenna; 349, mandible; 350, maxilla; 351, spiracular disk



MOLOPHILUS HIRTIPENNIS, PUPA

352, Female, lateral aspect; 353, male cauda, lateral aspect; 354, male cauda, dorsal aspect; 355, female cauda, lateral aspect; 356, female cauda, dorsal aspect

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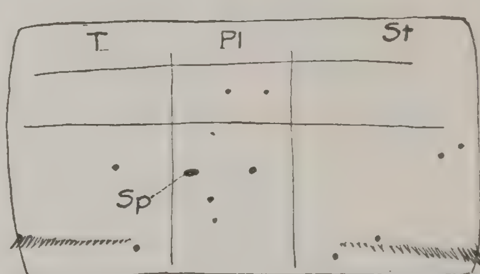

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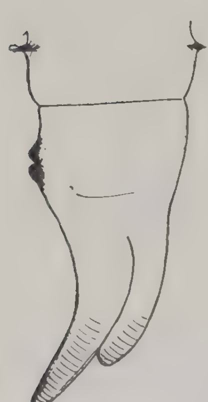


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ERIOPTERA MEGOPHTHALMA

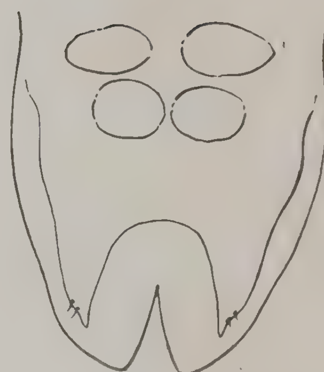
Larva: 357, spiracular disk; 358, anal gills, ventral aspect
Pupa: 359, female, lateral aspect; 360, female, ventral aspect; 361, fifth abdominal segment, lateral aspect (diagrammatic); 362, male cauda, lateral aspect; 363, male cauda, dorsal aspect

364 368 365 366 367

ERIOPTERA CHLOROPHYLLA, LARVA

364, Head capsule, showing bases of antennae; 365, mental bar; 366, aberration of mental bar; 367, antenna; 368, mandible


371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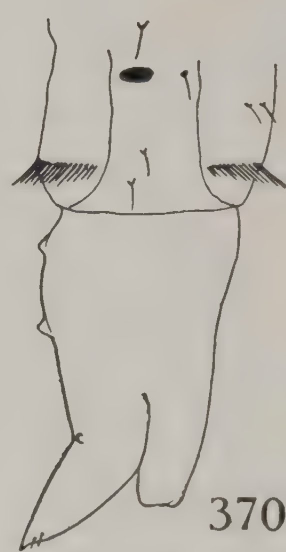
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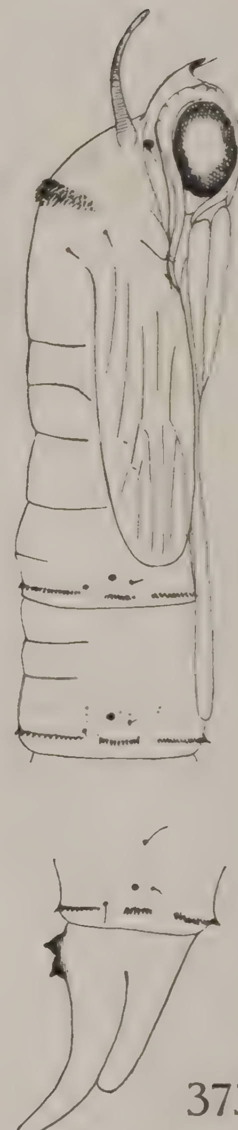
373

ERIOPTERA CHLOROPHYLLA, E. SEPTEMTRIONIS, AND E. ARMATA

Erioptera chlorophylla, pupa: 369, female, lateral aspect; 370, female cauda, lateral aspect

Erioptera septemtrionis, pupa: 371, male cauda, lateral aspect; 372, male cauda, dorsal aspect

Erioptera armata, pupa: 373, female, lateral aspect

375

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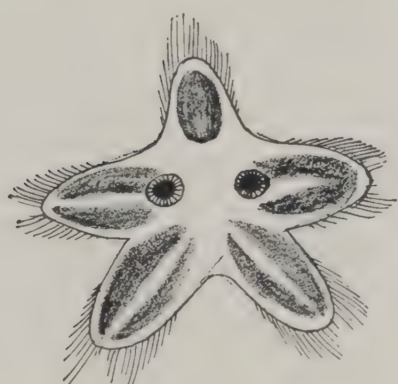

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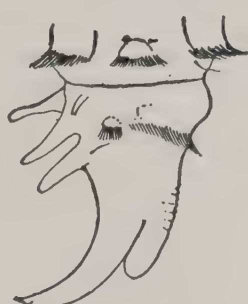

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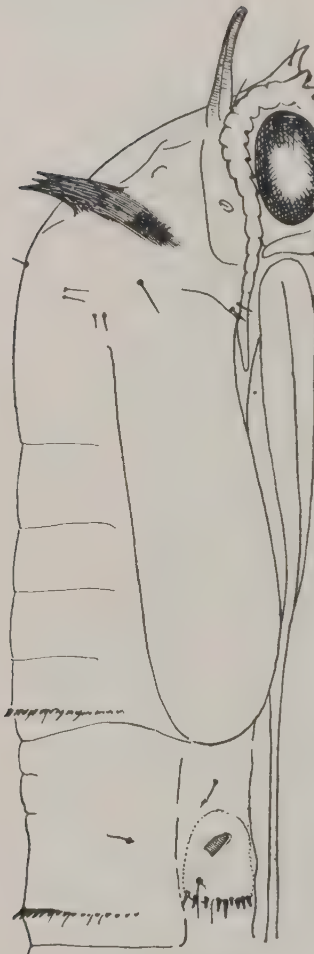
378

ORMOSIA NUBILA, O. INNOCENS, AND O. MEIGENII

Ormosia nubila, larva: 374, mandible; 375, spiracular disk

Ormosia innocens, pupa: 376, female, lateral aspect; 377, male cauda, dorsal aspect; 378, male cauda, lateral aspect

Ormosia meigenii, larva: 379, spiracular disk



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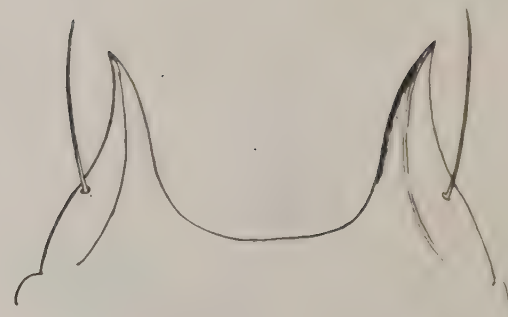

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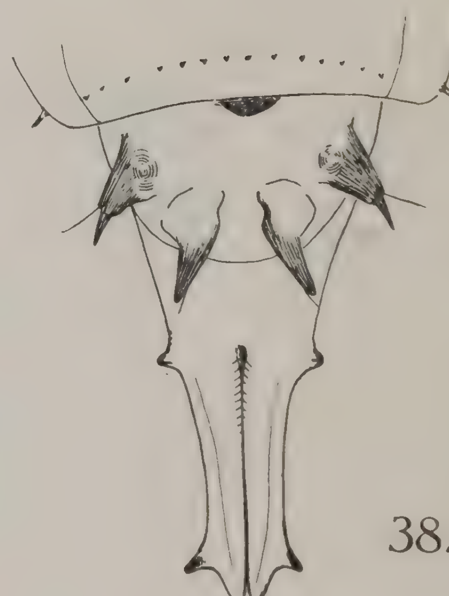
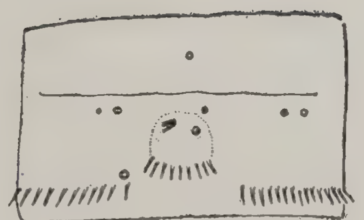


382

ORMOSIA NUBILA, PUPA

380, Female, lateral aspect; 381, cephalic crest of female, ventral aspect; 382, female cauda, dorsal aspect



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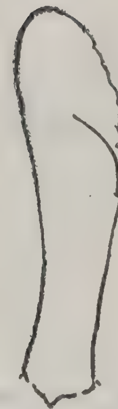

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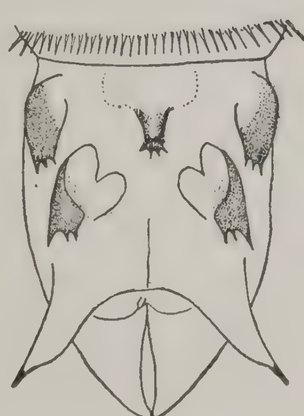

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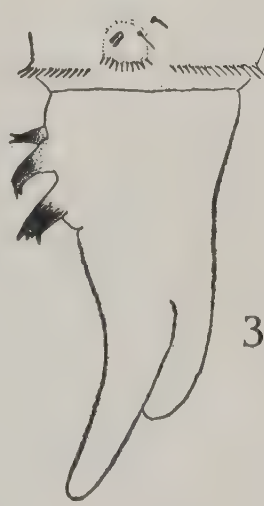
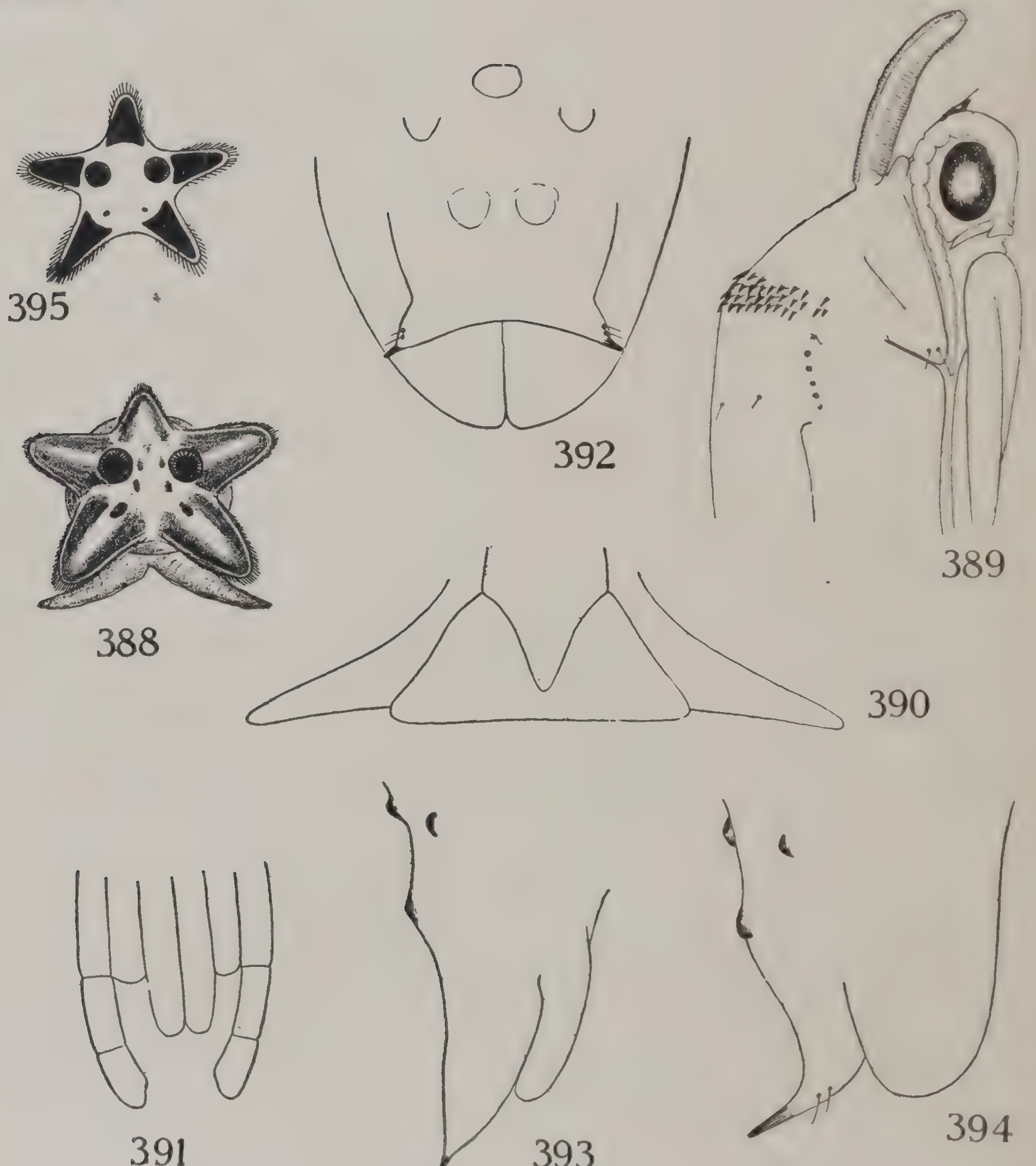


387

ORMOSIA NIGRIPILA, PUPA

383, Male, lateral aspect; 384, pronotal breathing horn; 385, fifth abdominal segment, lateral aspect (diagrammatic); 386, male cauda, dorsal aspect; 387, female cauda, lateral aspect

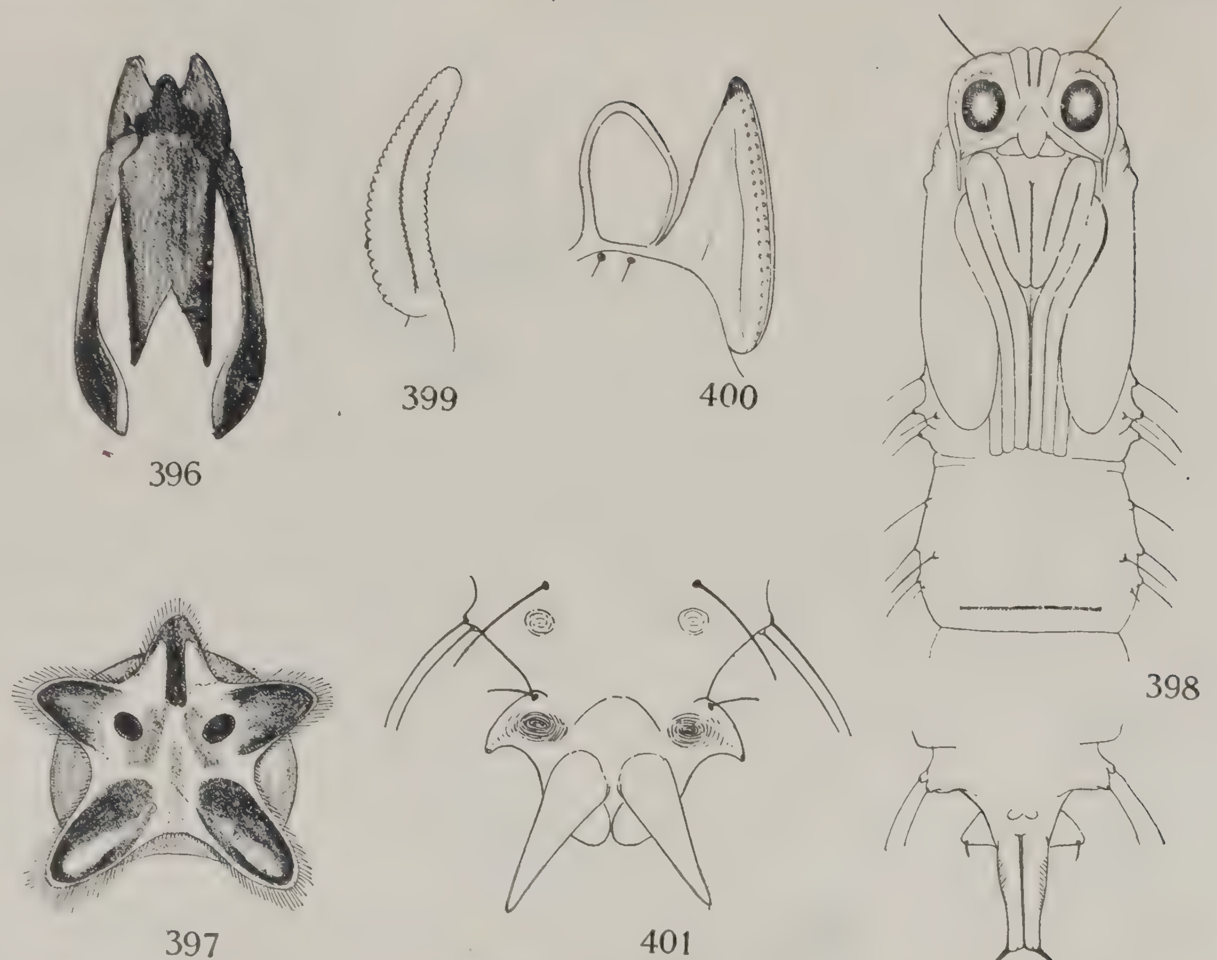


HELOBIA HYBRIDA AND TRIMICRA PILIPES

Helobia hybrida, larva: 388, spiracular disk

Helobia hybrida, pupa: 389, female, lateral aspect; 390, mouth parts; 391, arrangement of leg sheaths; 392, male cauda, dorsal aspect; 393, female cauda, lateral aspect; 394, male cauda, lateral aspect

Trimicra pilipes, larva: 395, spiracular disk (after Gerbig)



GNOPHOMYIA TRISTISSIMA

Larva: 396, head capsule (after Malloch); 397, spiracular disk (after Malloch)
Pupa: 398, female, ventral aspect; 399, pronotal breathing horn, lateral aspect; 400, pronotal breathing horn and thoracic crest, dorsal aspect; 401, male cauda, dorsal aspect

403

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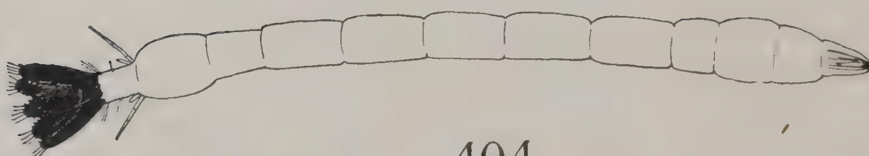

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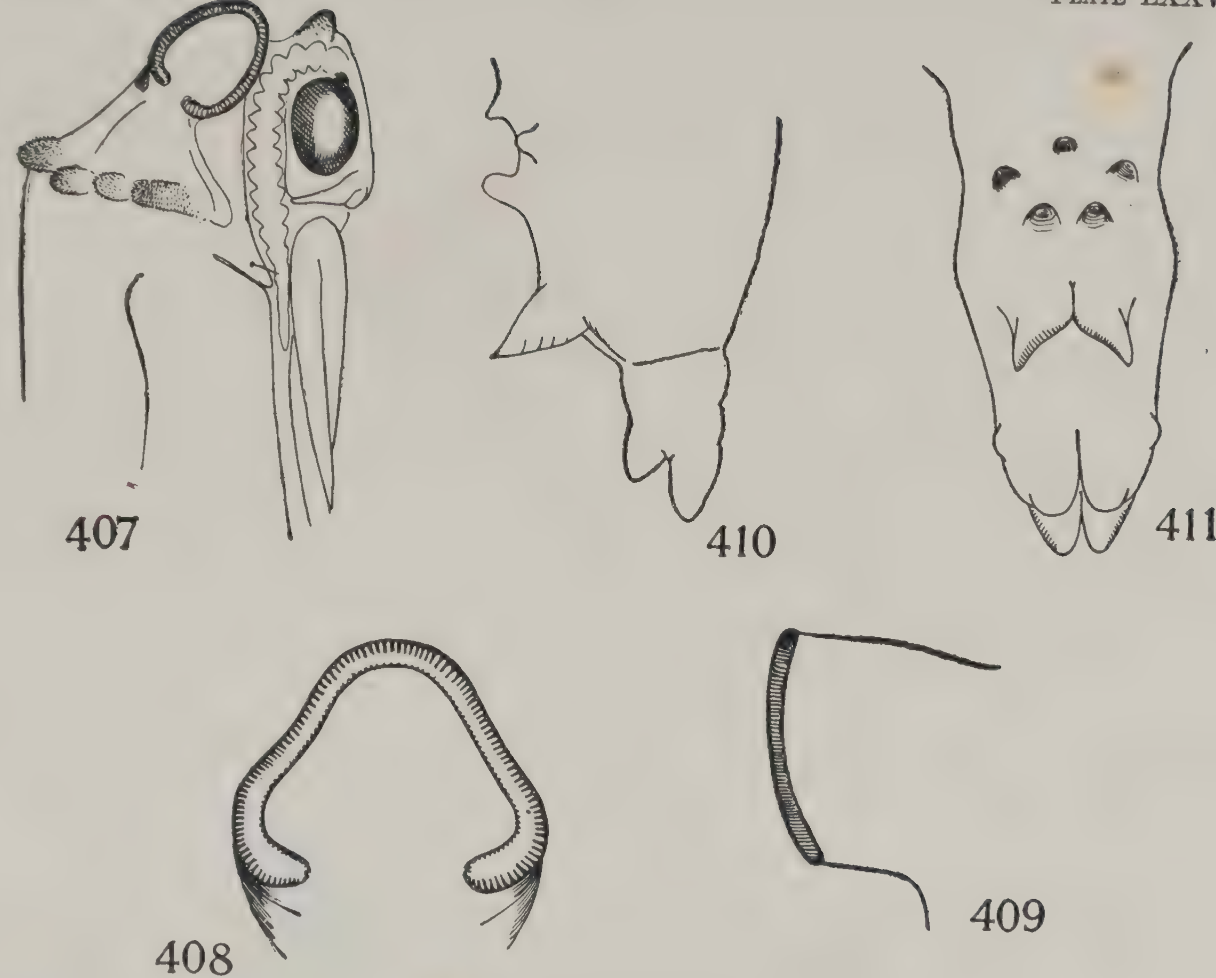
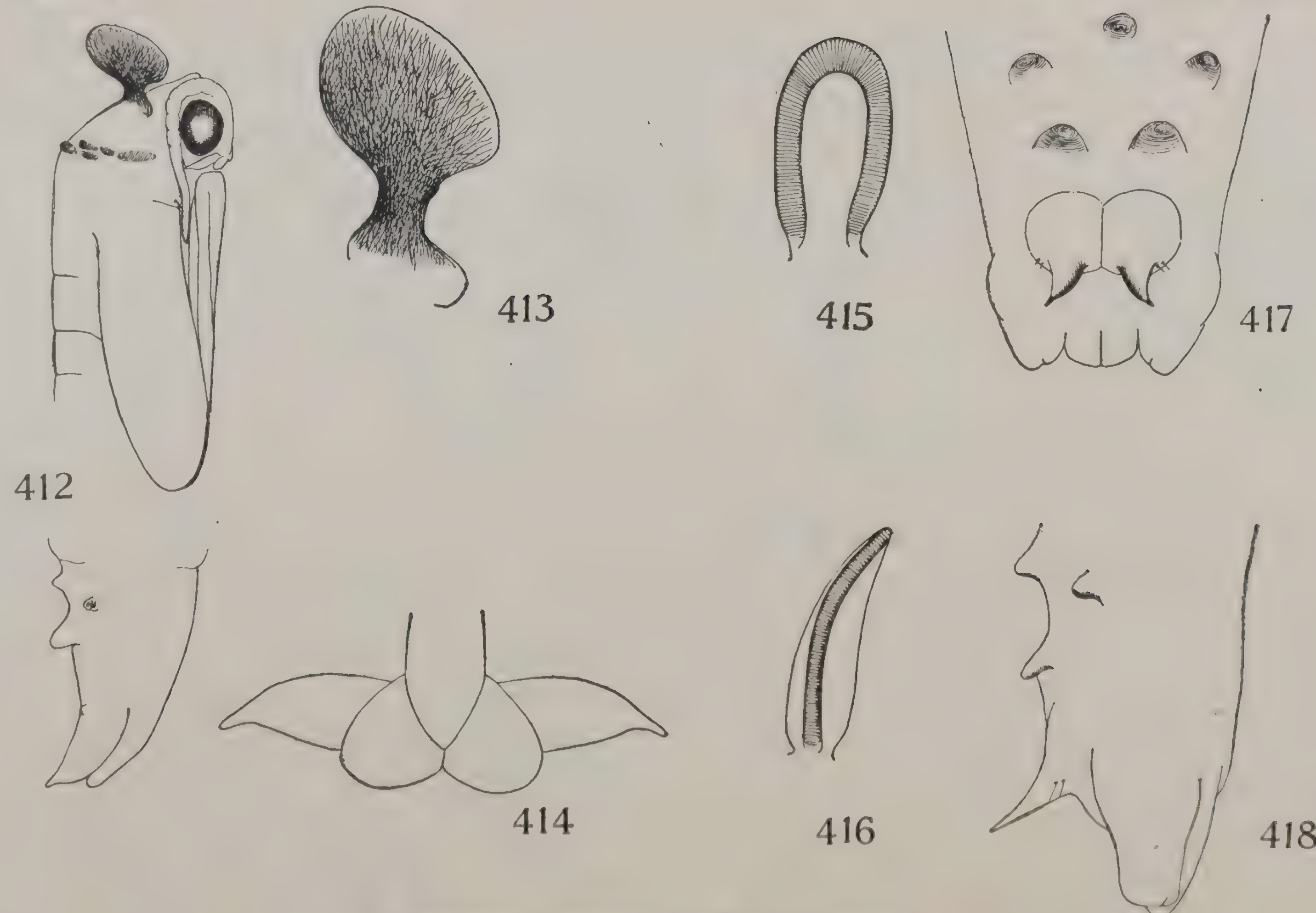
GONOMYIA ALEXANDERI AND ERIOPTERINE NO. 1

Gonomyia alexanderi, larva: 402, mandible; 403, spiracular disk
Eriopterine No. 1, larva: 404, lateral aspect; 405, spiracular disk and anal gills; 406, lobe of spiracular disk, enlarged



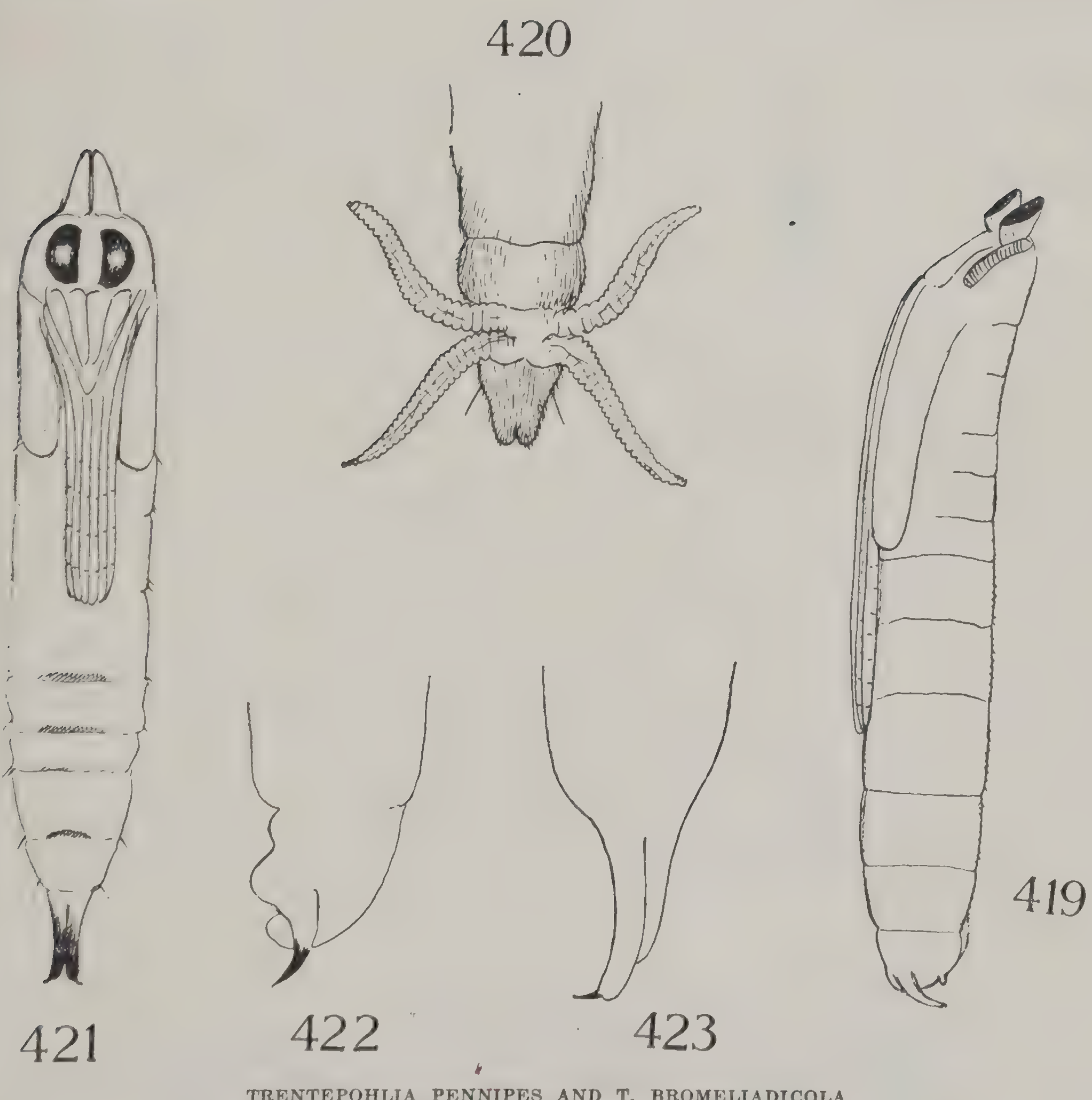
GONOMYIA ALEXANDERI, PUPA

407, Male, lateral aspect; 408, pronotal breathing horn; 409, pronotal breathing horn, lateral aspect; 410, male cauda, lateral aspect; 411, male cauda, dorsal aspect



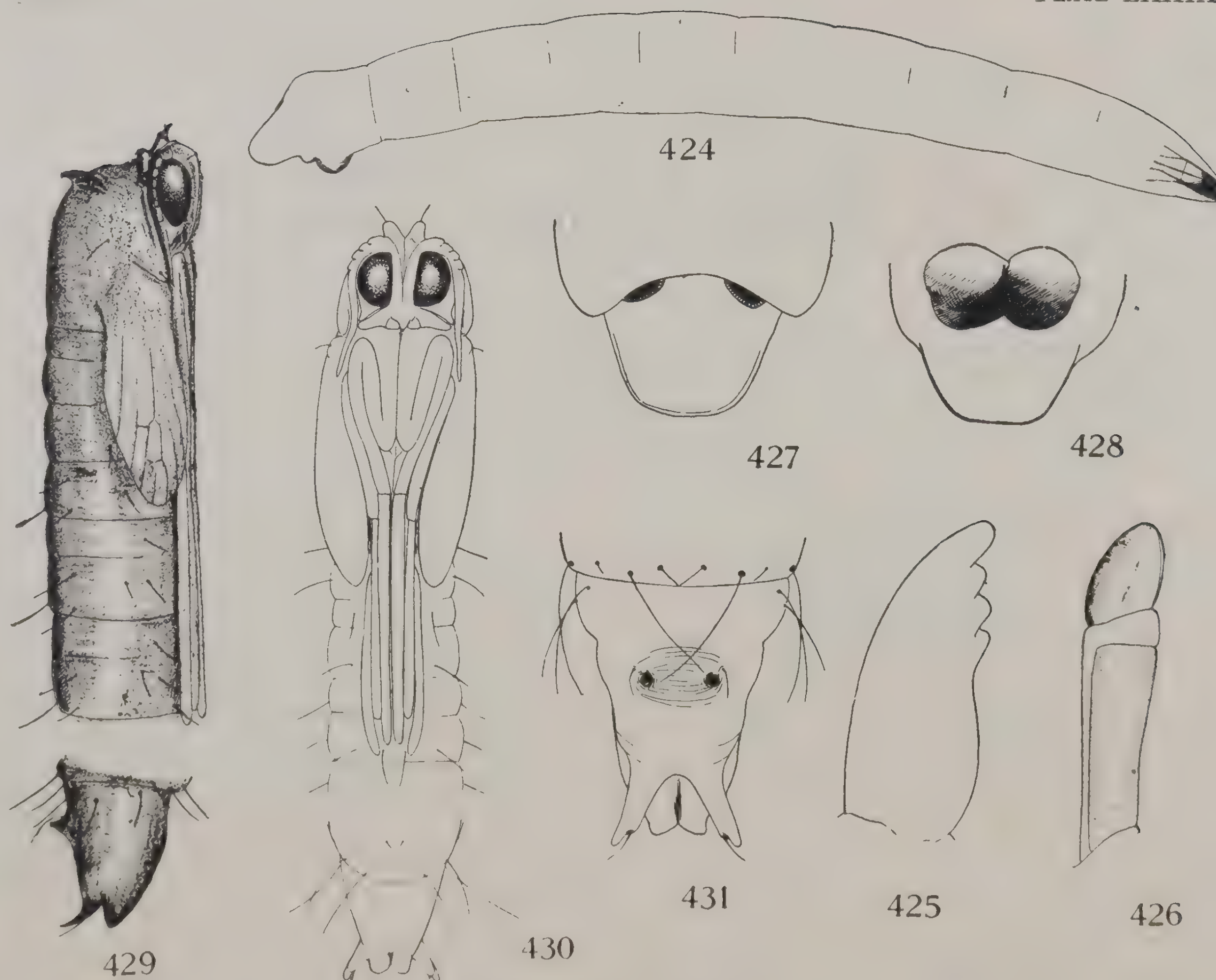
GONOMYIA SULPHURELLA AND G. KANSENSIS

Gonomyia sulphurella, pupa: 412, female, lateral aspect; 413, pronotal breathing horn, lateral aspect; 414, mouth parts *Gonomyia kansensis*, pupa: 415, pronotal breathing horn, lateral aspect; 416, pronotal breathing horn, ventral aspect; 417, male cauda, dorsal aspect; 418, male cauda, lateral aspect



TRENTEPOHLIA PENNIPES AND T. BROMELIADICOLA

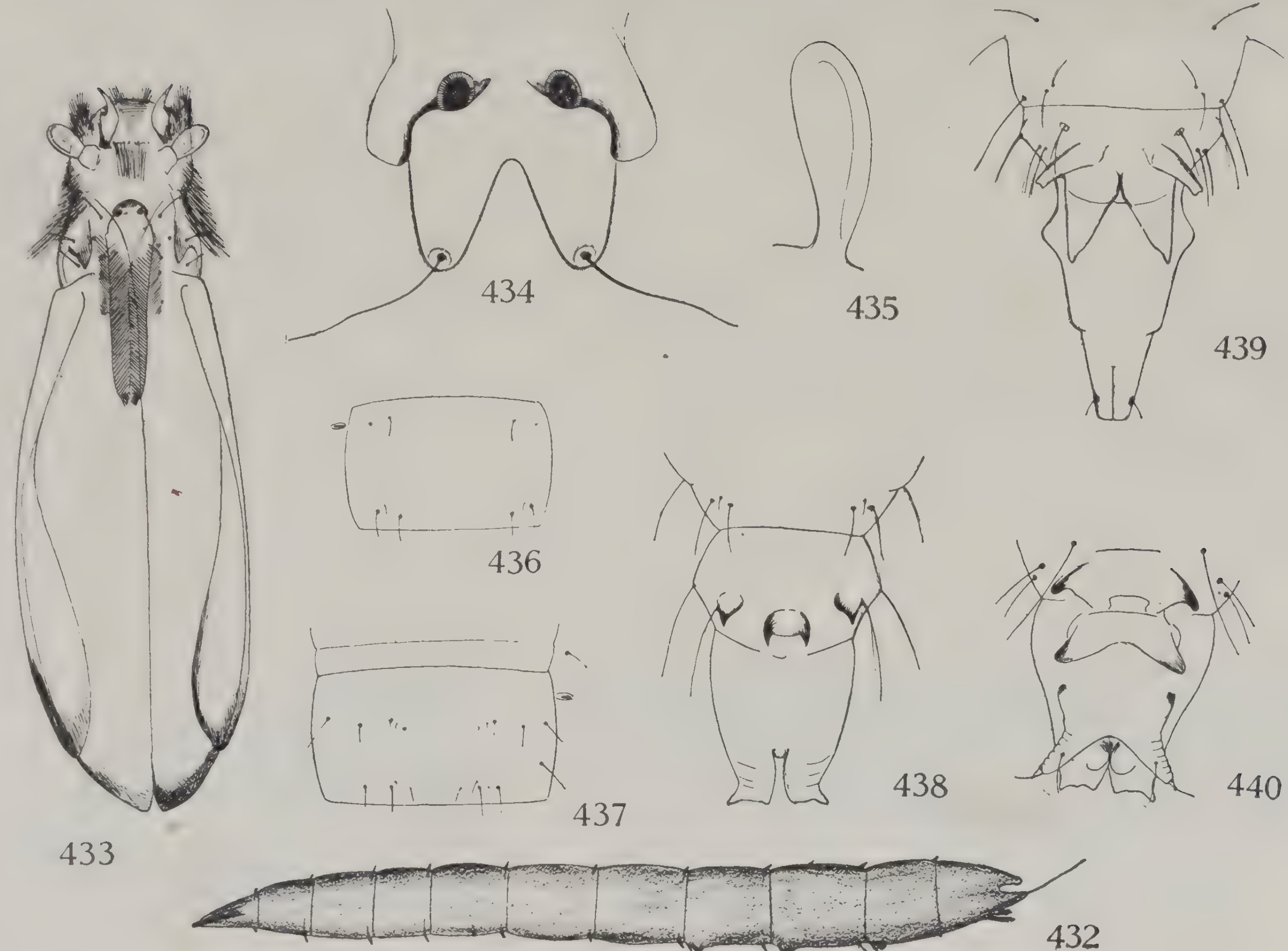
Trentepohlia pennipes, pupa: 419, lateral aspect (after De Meijere)
Trentepohlia bromeliadicola, larva (after Picado): 420, anal gills
Trentepohlia bromeliadicola, pupa (after Picado): 421, female, ventral aspect; 422, male cauda, lateral aspect; 423, female cauda, lateral aspect



TEUCHOLABIS COMPLEXA

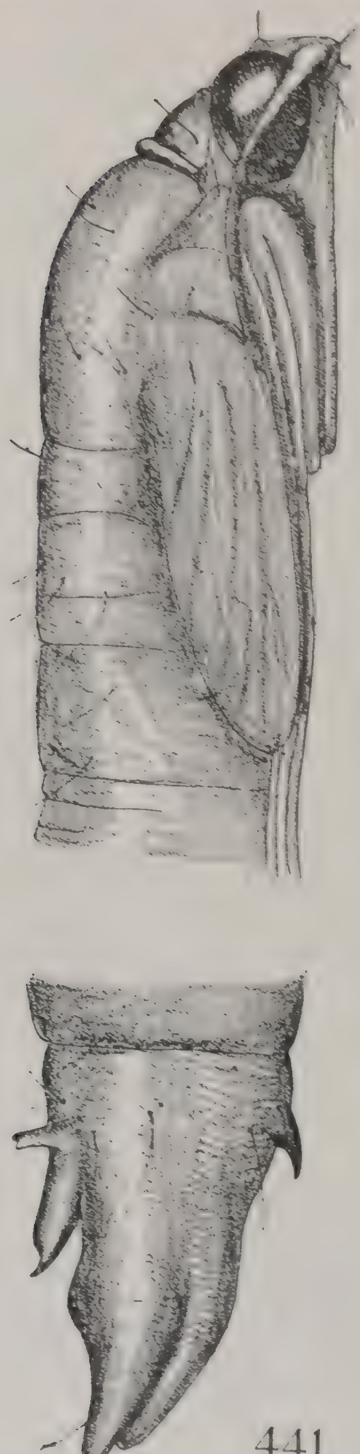
Larva: 424, lateral aspect; 425, mandible; 426, antenna; 427, spiracular disk, dorsal aspect; 428, anal gills

Pupa: 429, male, lateral aspect; 430, male, ventral aspect; 431, male cauda, dorsal aspect



ELEPHANTOMYIA WESTWOODI

Larva: 432, lateral aspect; 433, head capsule, ventral aspect; 434, spiracular disk, dorsal aspect
Pupa: 435, pronotal breathing horn; 436, fifth abdominal segment, ventral aspect (diagrammatic); 437, fifth abdominal segment, dorsal aspect; 438, male cauda, ventral aspect; 439, female cauda, dorsal aspect; 440, male cauda, dorsal aspect



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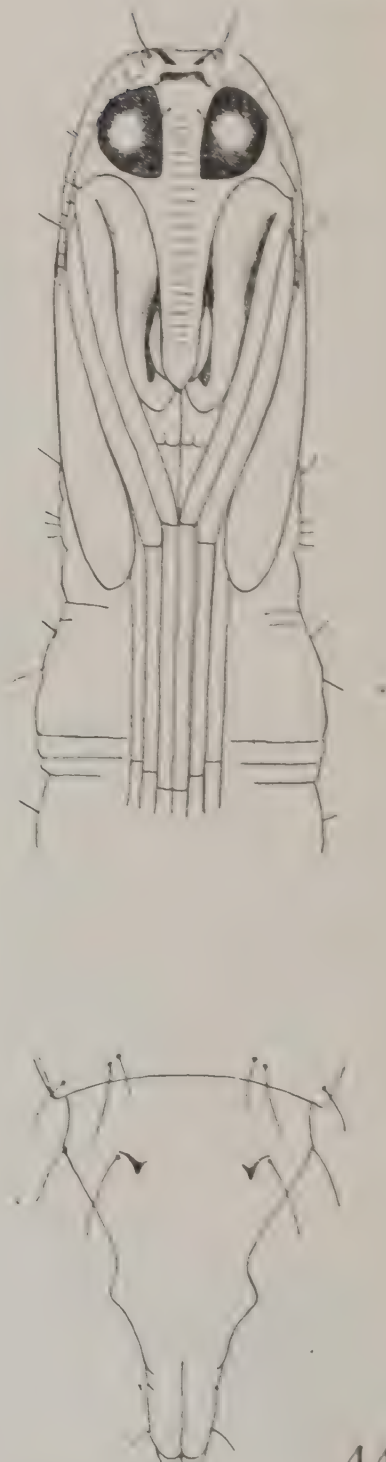
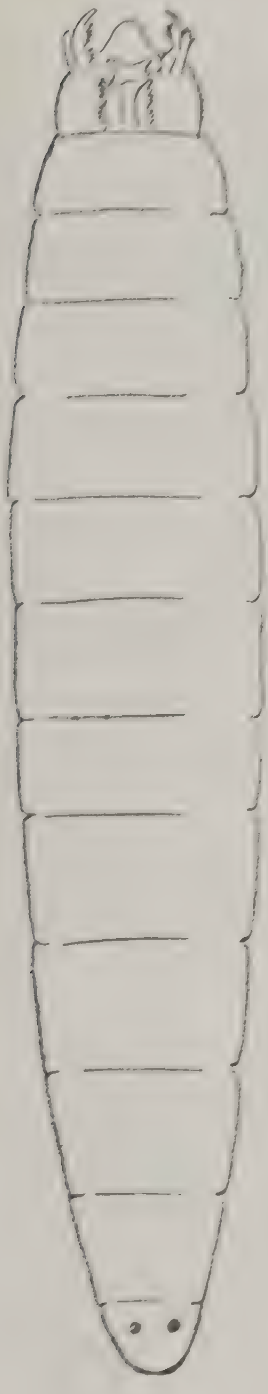


442

ELEPHANTOMYIA WESTWOODI, PUPA

441, Female, lateral aspect; 442, female, ventral aspect



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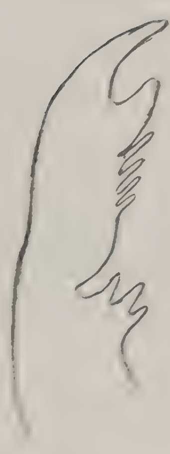

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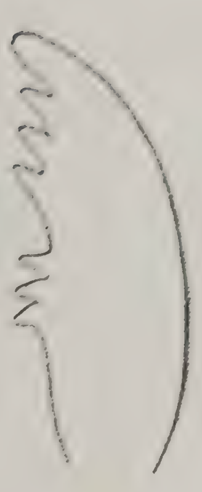

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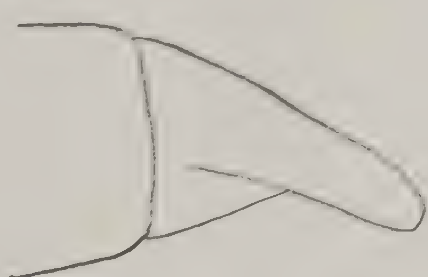

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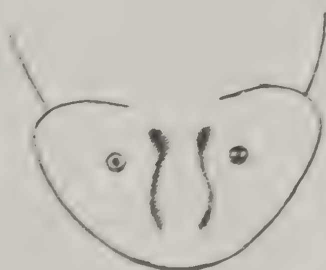
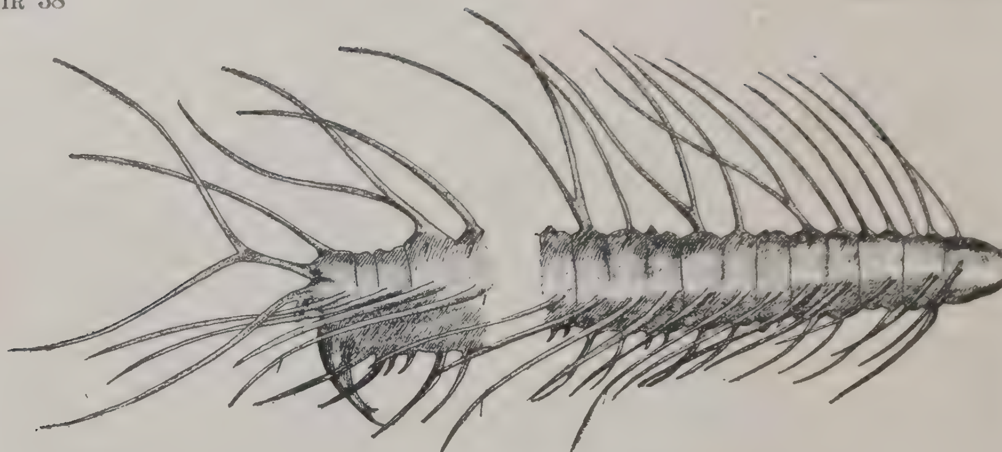


447

CHIONEA ARANEOIDES, LARVA (AFTER BRAUER)

443, Dorsal aspect; 444, mandible; 445, possibly mental plate; 446, spiracular disk, lateral aspect; 447, spiracular disk, dorsal aspect



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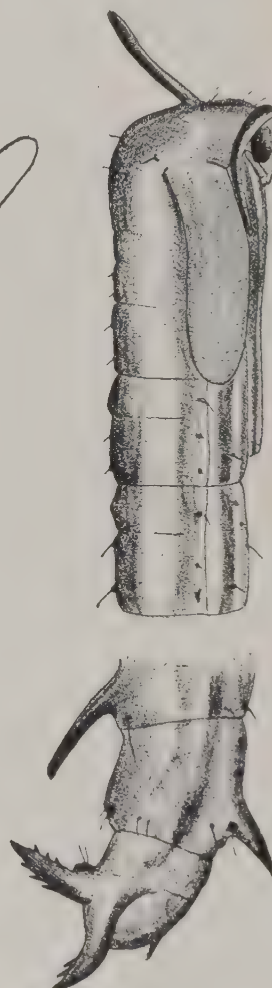

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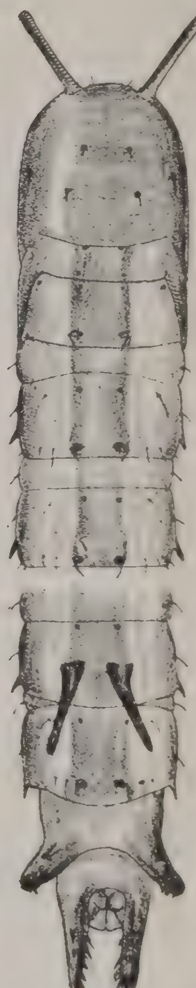


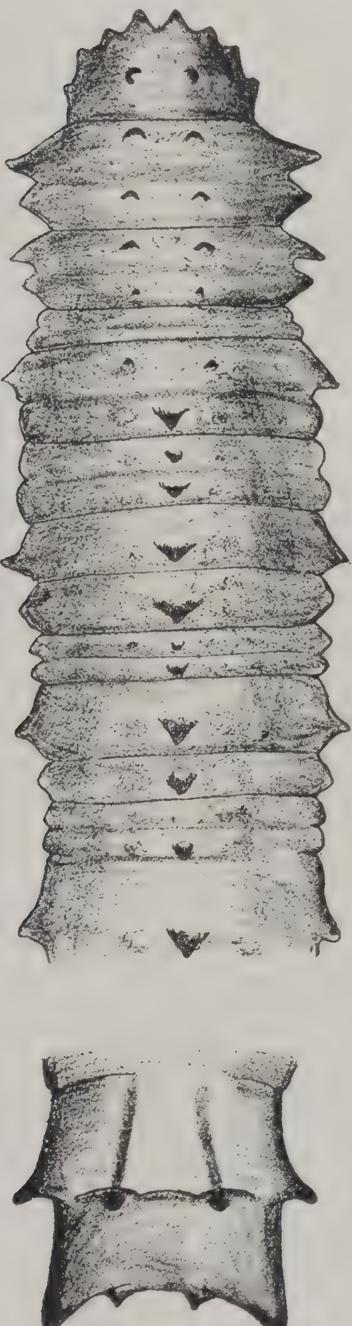
450

PHALACROCERA REPLICATA AND TRIOGMA TRISULCATA

Phalacrocera replicata, larva: 448, lateral aspect

Phalacrocera replicata, pupa: 449, male, lateral aspect; 450, male, dorsal aspect; 451, mouth parts

Triogma trisulcata: 452, larva (after Steinmann)



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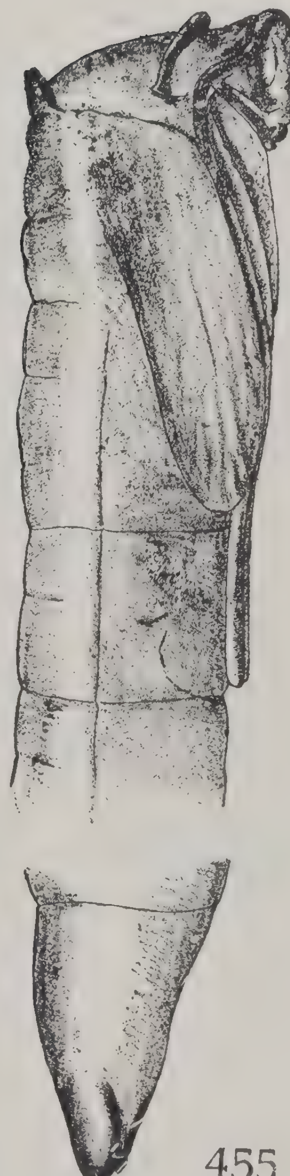

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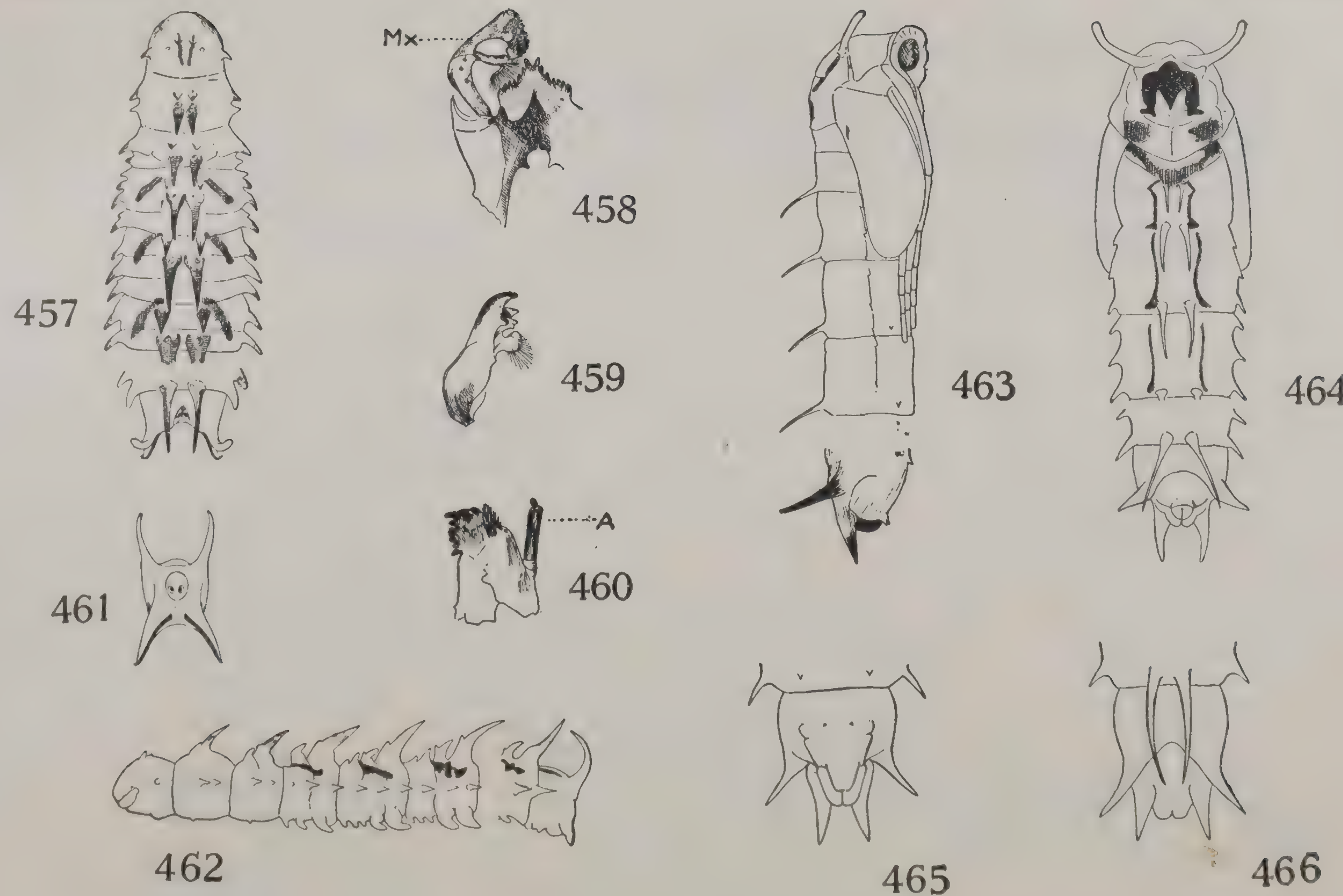
456

CYLINDROTOMA SPLENDENS

Larva: 453, dorsal aspect; 454, mandible
Pupa: 455, female, lateral aspect; 456, head of female, ventral aspect

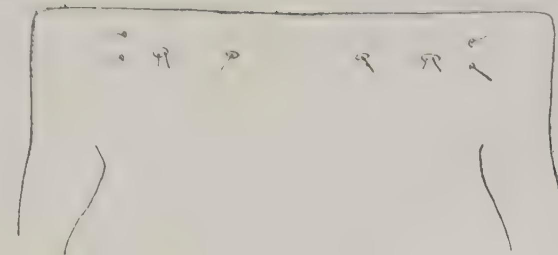


LIOGMA NODICORNIS

Larva: 457, dorsal aspect; 458, mentum and maxilla; 459, mandible; 460, mandible and antenna; 461, spiracular disk; 462, lateral aspect of larva

Pupa: 463, male, lateral aspect; 464, male, dorsal aspect; 465, female cauda, ventral aspect; 466, female cauda, dorsal aspect

469



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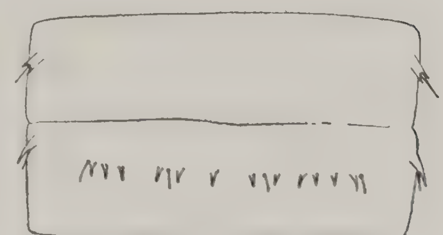

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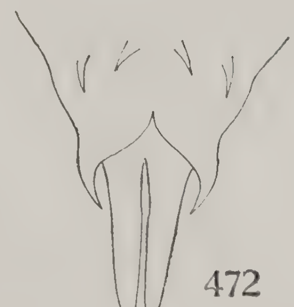

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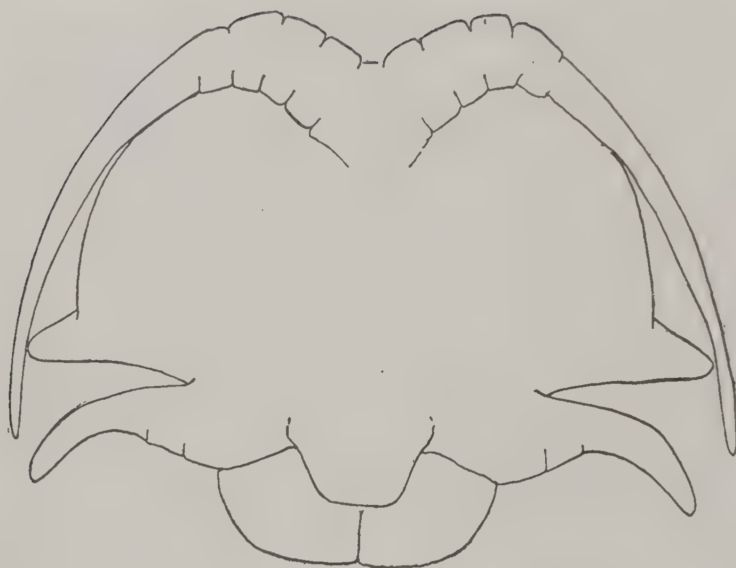
473

OROPEZA OBSCURA

Larva: 467, mentum; 468, hypopharynx; 469, spiracular disk
Pupa: 470, metanotum (diagrammatic); 471, fifth abdominal tergite (diagrammatic); 472, female cauda, dorsal aspect; 473, female cauda, ventral aspect



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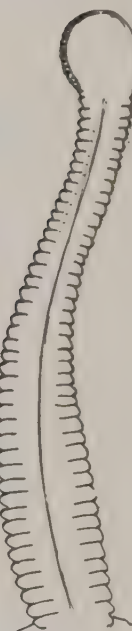

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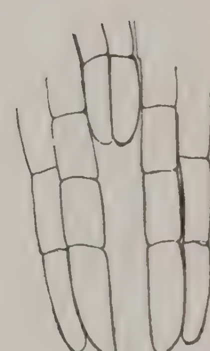

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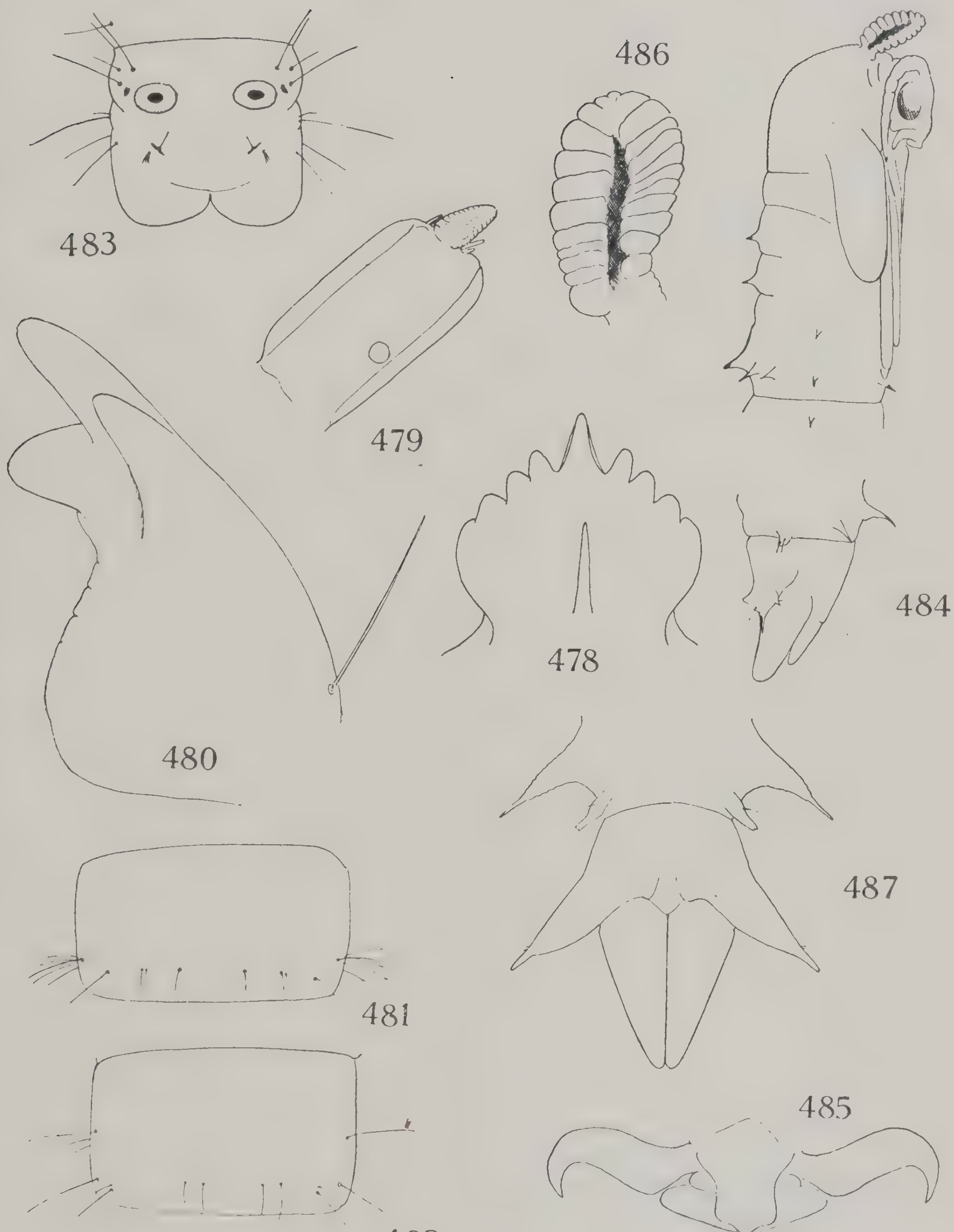
BRACHYPREMNA DISPELLENS, PUPA

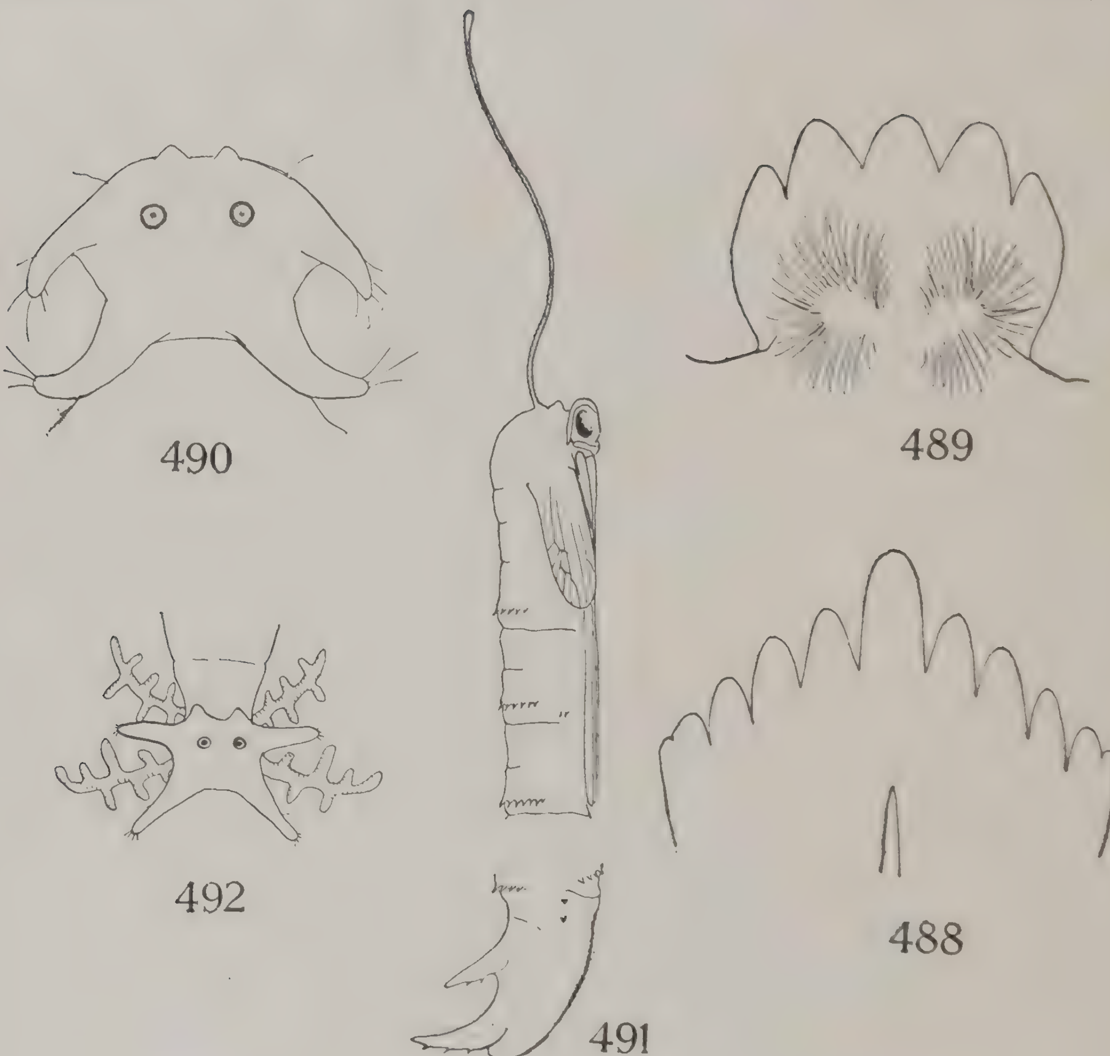
474, Head, ventral aspect; 475, pronotal breathing horn; 476, arrangement of leg sheaths; 477, male cauda, ventral aspect



TANYPTERA FRONTALIS

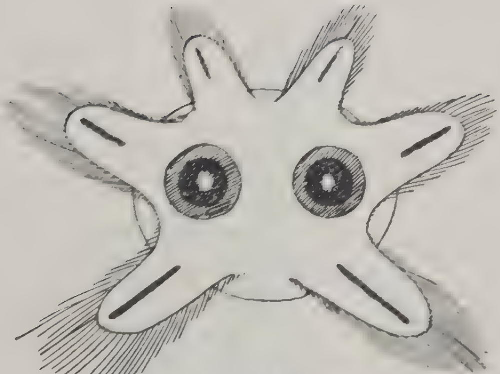
Larva: 478, mentum; 479, antenna; 480, mandible; 481, fifth abdominal segment, dorsal aspect (diagrammatic); 482, fifth abdominal segment, ventral aspect (diagrammatic); 483, spiracular disk

Pupa: 484, female, lateral aspect; 485, mouth parts; 486, pronotal breathing horn; 487, female cauda, dorsal aspect



LONGURIO TESTACEUS AND AESHNASOMA RIVERTONENSIS

Longurio testaceus, larva: 488, mentum; 489, hypopharynx; 490, spiracular disk
Longurio testaceus, pupa: 491, male, lateral aspect
Aeshnasoma rivertonensis, larva: 492, spiracular disk, showing branched anal gills (after Johnson)



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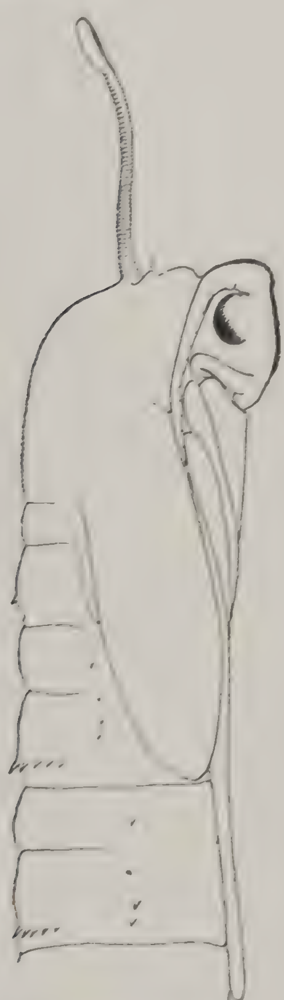

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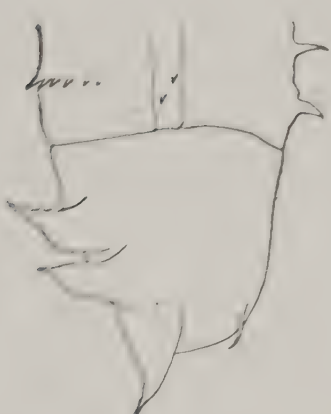

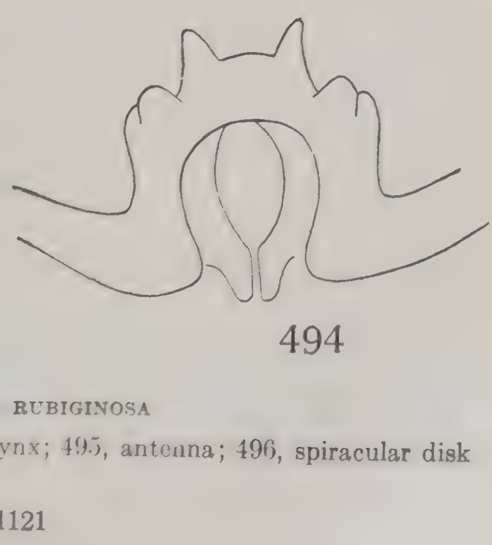

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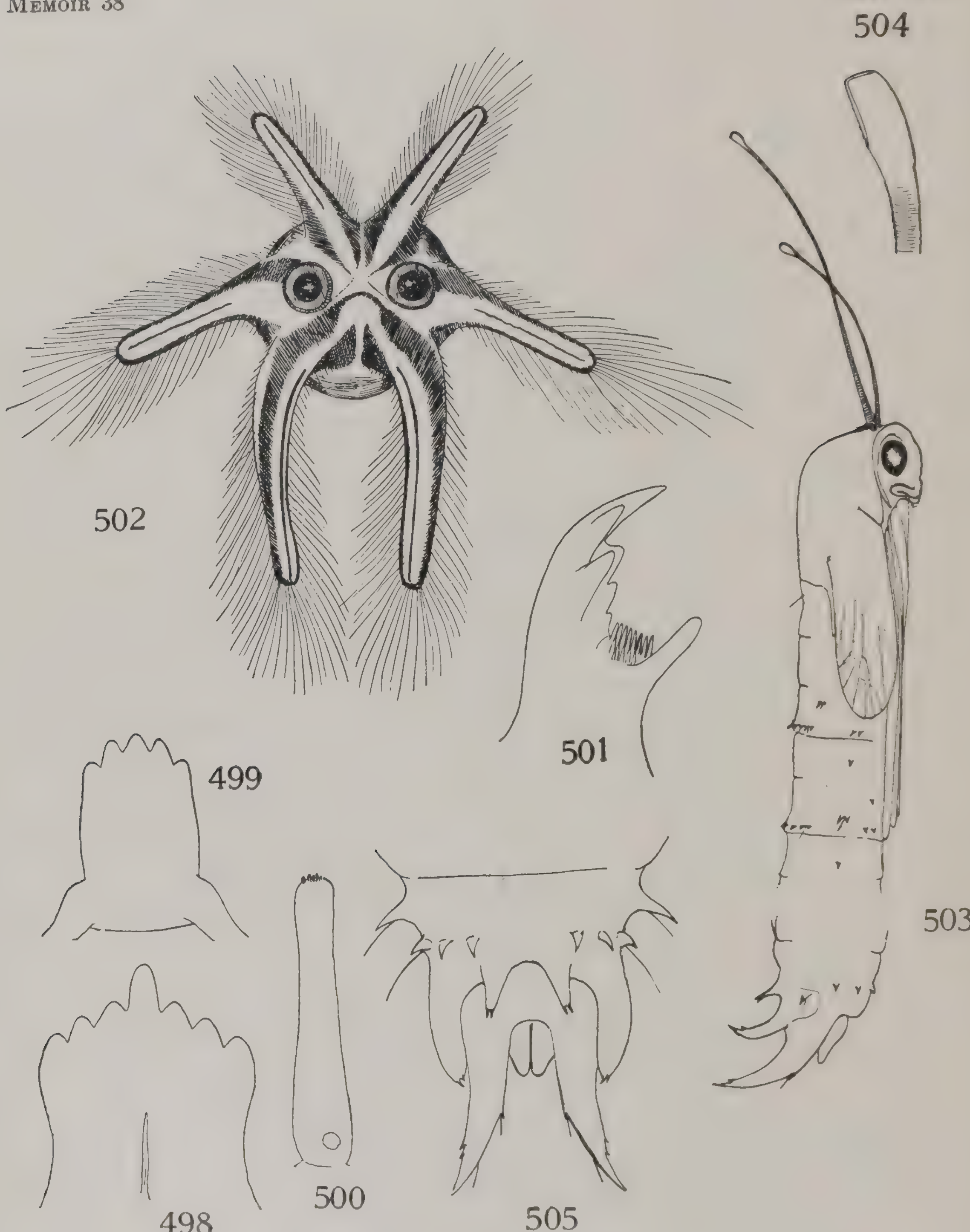
HOLORUSIA RUBIGINOSA

Larva: 493, mentum; 494, hypopharynx; 495, antenna; 496, spiracular disk
Pupa: 497, male, lateral aspect

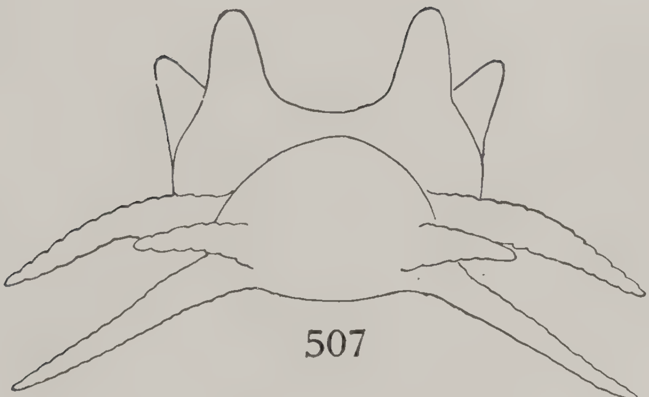


PRIONOCERA FUSCIPENNIS

Larva: 498, mentum; 499, hypopharynx; 500, antenna; 501, mandible; 502, spiracular disk

Pupa: 503, lateral aspect; 504, tip of pronotal breathing horn; 505, male cauda, dorsal aspect

506



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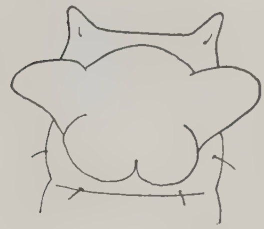

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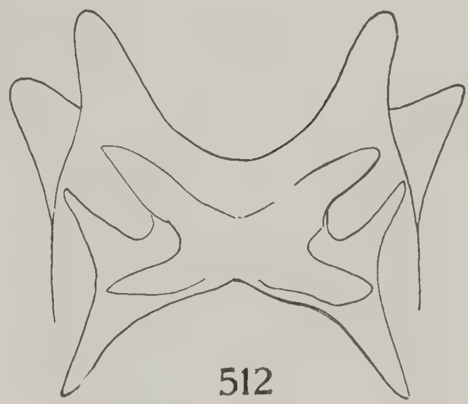

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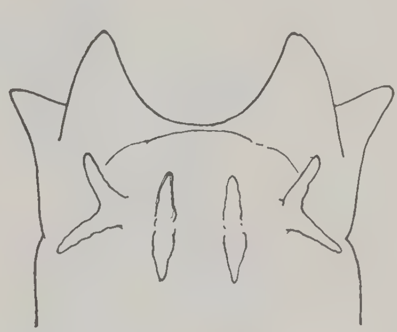
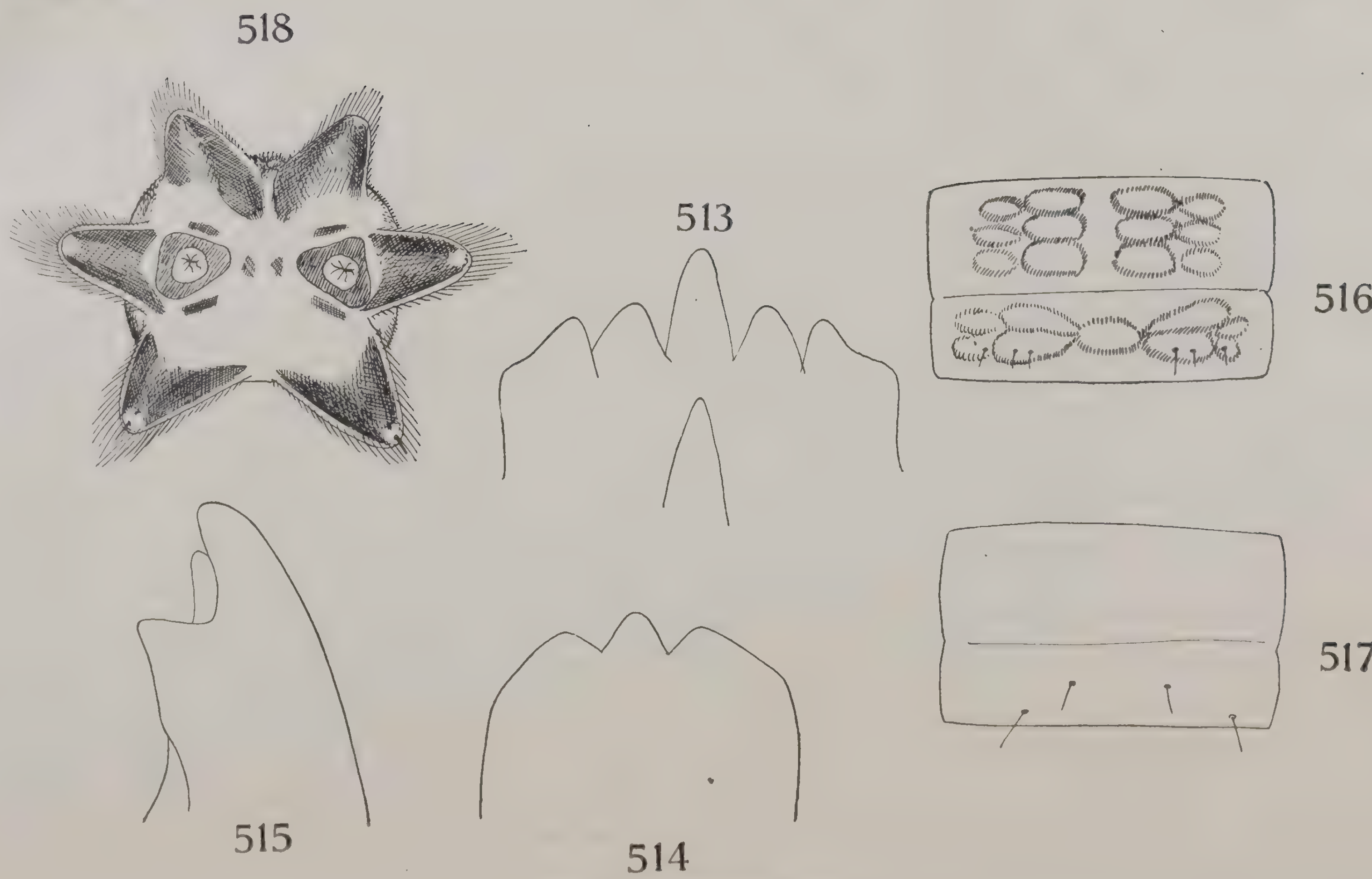


511

TYPES OF ANAL GILLS IN GENUS TIPULA, VENTRAL ASPECT

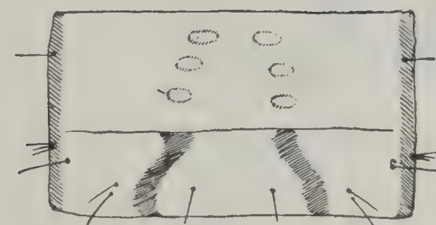
506, *Tipula oropezoides*; 507, *T. nobilis*; 508, *T. caloptera*; 509, *T. dejecta*; 510, *T. usitata*; 511, *T. ignobilis*; 512, *T. iroquois* (supposition)



TIPULA OROPEZOIDES, LARVA

513, Mentum; 514, hypopharynx; 515, mandible; 516, fifth abdominal segment, dorsal aspect; 517, fifth abdominal segment, ventral aspect; 518, spiracular disk

520



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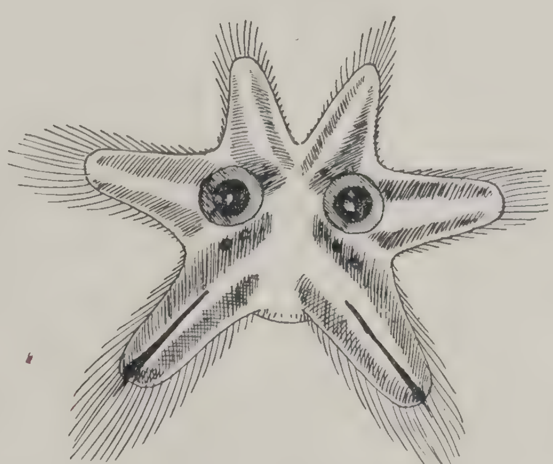

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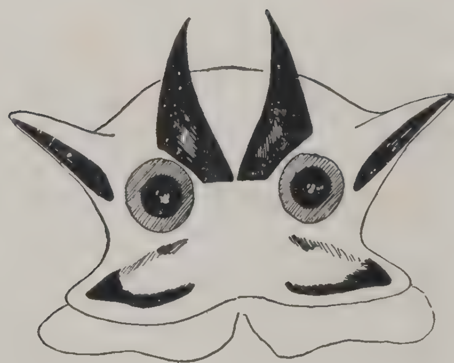
522

TIPULA COLLARIS

Larva: 519, mentum; 520, hypopharynx; 521, fifth abdominal segment, dorsal aspect; 522, spiracular disk

Pupa: 523, male, lateral aspect



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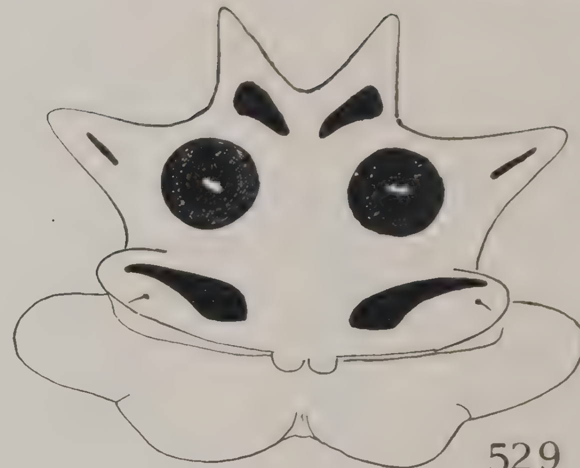

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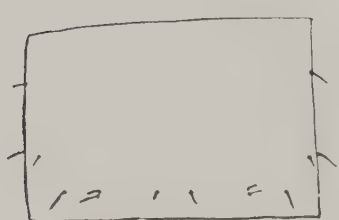

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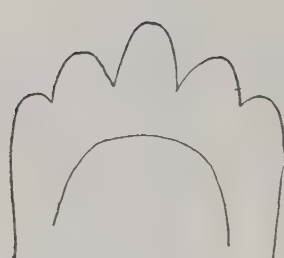

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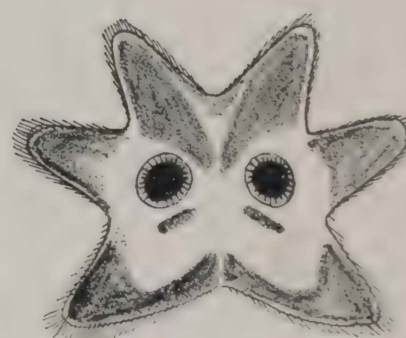

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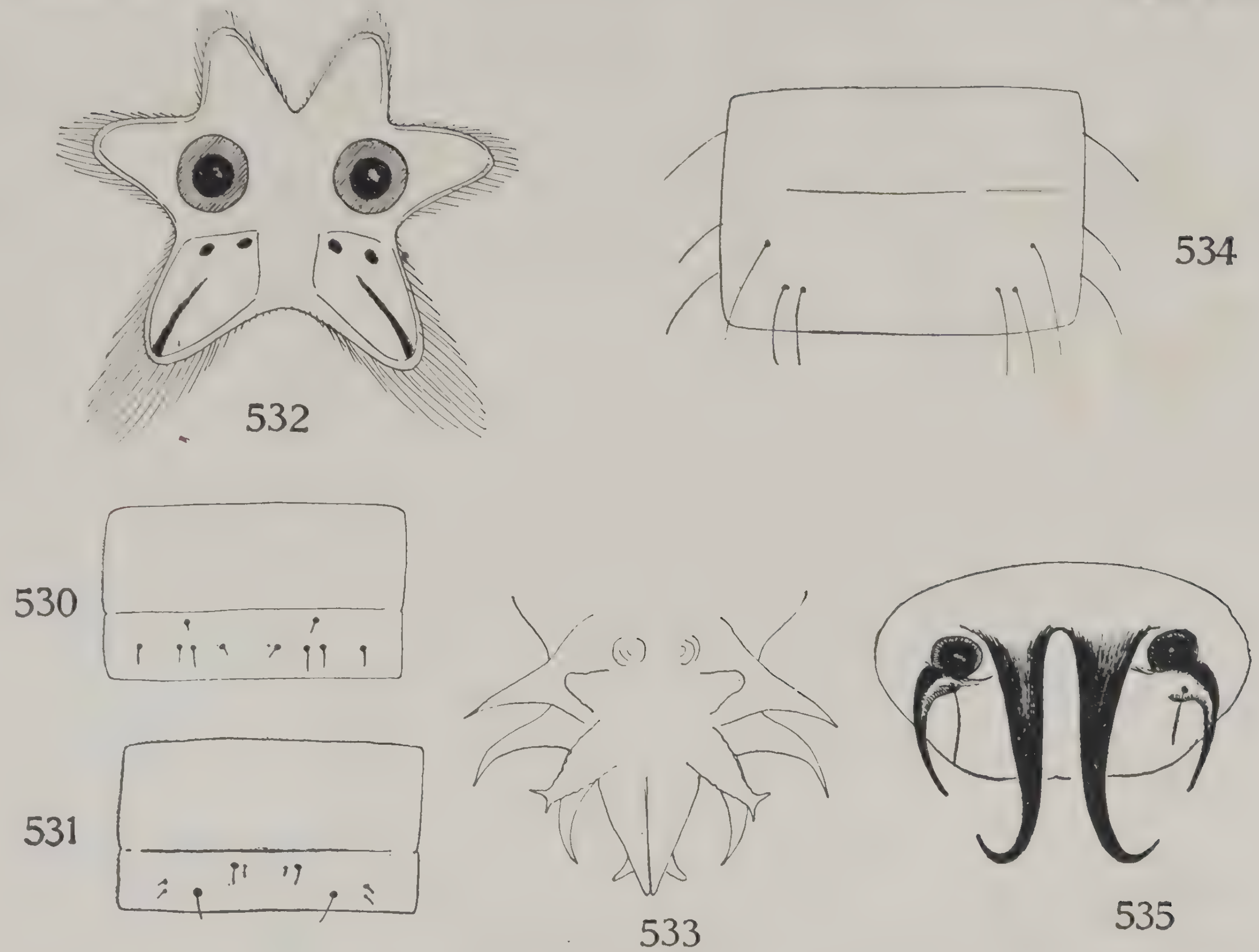
TIPULA DEJECTA, T. USITATA, AND T. TRIVITTATA

Tipula dejecta, larva: 524, mentum; 525, hypopharynx; 526, spiracular disk
Tipula usitata, larva: 527, fifth abdominal segment, dorsal aspect; 528, spiracular disk
Tipula trivittata, larva: 529, spiracular disk

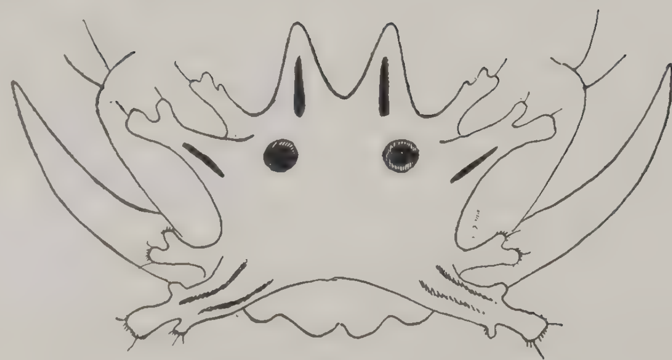


TIPULA IGNOBILIS AND TIPULINE NO. 2

Tipula ignobilis, larva: 530, fifth abdominal segment, dorsal aspect; 531, fifth abdominal segment, ventral aspect; 532, spiracular disk

Tipula ignobilis, pupa: 533, female cauda, dorsal aspect

Tipuline No. 2, larva: 534, fifth abdominal segment, dorsal aspect; 535, spiracular disk



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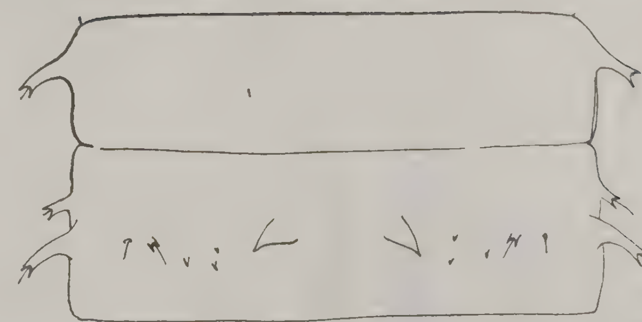

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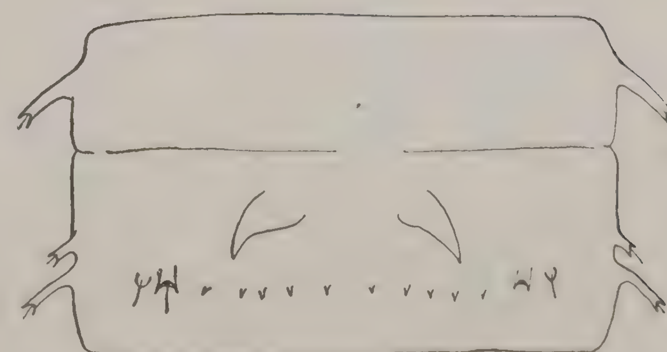

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TIPULA ABDOMINALIS

Larva: 536, mentum; 537, spiracular disk
Pupa: 538, fifth abdominal tergite; 539, fifth abdominal sternite

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